Succession versus grazing:
effects on the vegetation of inland sand ecosystems

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Süss, K., Storm, C., Zimmermann, K. & Schwabe, A. The interrelationship between productivity, plant species richness and livestock diet: a question of scale? *(submitted)*

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Süss, K. & Schwabe, A. Sheep versus donkey grazing or mixed treatment: results from a 4-year field experiment in Armerio-Festucetum trachyphyllae sand vegetation *(submitted)*

In Bearbeitung

Süss, K., Bergmann, S. & Storm, C. How does nutrient addition affect the pioneer grassland vegetation of calcareous inland sand-ecosystems?

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Süss, K. 2004. Fraß- und Raumnutzungsverhalten bei sukzessiver Multispecies-Beweidung mit Wiederkäuern (Schafe) und Nicht-Wiederkäuern (Esel) in Sandökosystemen. In: Schwabe, A. & Kratochwil, A. (eds.): Beweidung und Restitution als Chancen für den Naturschutz? NNA-Berichte 17 (1): 127-132. Norddeutsche Naturschutzakademie, Schneverdingen.

Zehm, A., **Süss,** K., Eichberg, C. & Häfele, S. 2004. Effekte der Beweidung mit Schafen, Eseln und Wollschweinen auf die Vegetation von Sand-Ökosystemen. - In: Schwabe, A. & Kratochwil, A. (eds.): Beweidung und Restitution als Chancen für den Naturschutz? NNA-Berichte 17 (1): 111-126. Norddeutsche Naturschutzakademie, Schneverdingen.

Schwabe, A., Zehm, A., Nobis, M., Storm, C. & **Süss**, K. 2004. Auswirkungen von Schaf-Erstbeweidung auf die Vegetation primär basenreicher Sand-Ökosysteme. In: Schwabe, A. & Kratochwil, A. (eds.): Beweidung und Restitution als Chancen für den Naturschutz? NNA-Berichte 17 (1): 39-54. Norddeutsche Naturschutzakademie, Schneverdingen.

Kongress-Abstracts

Süss, K., Schwabe, A., Storm, C. & Zehm, A. 2004. Restorative grazing as a tool against species-poor stages with „grass-encroachment“. Verhandlungen der Gesellschaft für Ökologie 34: 163.

Contents

Chapter 1:
General introduction

In recent years, a decrease of diversity accompanied by a ruderalisation tendency has been reported for many ecosystem types (Welch & Scott 1995, de Bonte et al. 1999, Hölzel & Otte 2003, Bischoff 2005). Besides other factors, the abandonment of former land-use is considered as one presumable cause for habitat-loss which leads to the decrease of site-specific plant species (Schwabe et al. 2004, Bielsa et al. 2005). Without stochastic processes of disturbance, succession can lead to an increase of tall grasses and shrub species (Bakker 2005). According to the "competitive stress-tolerance ruderal" CSR-model of Grime (1979) mainly competitors or ruderals increase at the expense of site-specific specialists, mainly stress-tolerators.

Besides the changes in agricultural land-use, also an increasing nitrogen immission can be a reason for the spreading abundance of ubiquitous plants, which are often dominant nitrophytes (Kooijman & van der Meulen 1996, ten Harkel et al. 1995, de Bonte et al. 1999). Hence competitors and ruderals become a matter of great concern (Bakker 2005). Numerous studies have developed a better understanding of ecosystem functioning and maintenance management for aims of nature conservation in a variety of ecosystems (e.g. Loreau et al. 2001, Hector et al. 2001).

For low-productivity ecosystems many management methods have been discussed, e.g., mowing, grazing, burning and others (e.g. Moog et al. 2002). As might be expected from the former traditional influence of livestock during the extensive land-use of past centuries, grazing has turned out to be an effective tool of nature conservation for these ecosystems (Stroh et al. 2002, Hellström et al. 2003).

In this study, inland sand ecosystems served as a model for dry low-productivity pioneer stages and grassland. Especially the open, early successional stages, during which many poorly competitive plant species thrive, are among the endangered habitats in Central Europe (Schwabe et al. 2002), and plant communities belonging to the Koelerion glaucae vegetation complex are characterised as threatened habitats according to the European conservation program Natura 2000 (Ssymank 1998). Sand ecosystems, mainly those on calcareous soils, are characterised by a high diversity of site-specific plant species - often stress-tolerators with adaptations to dry and nutrient-poor conditions. Therefore, these habitats are extremely sensitive to changes in agricultural land-use or nitrogen immission. The abandonment of extensive land-use can lead to progressive succession and the intensification of agricultural

use, to a high fertilisation impact. In recent decades both have resulted in a decrease of site-specific plants and only very recently, emphasis was placed on the maintenance management of sand ecosystems and the protection of early successional stages (e.g. Stroh et al. 2002).

Succession

The course and the driving factors of succession are still a matter of great concern in ecology and there have been many studies dealing with the theme of succession (Connell & Slatyer 1977, Tilman 1985, Huston & Smith 1987, Turner et al. 1998, Kahmen & Poschlod 2004). Abiotic factors, especially soil nitrogen content, have been considered to influence successional stages (Tilman 1987, Olff et al. 1993, Chapin III et al. 2002). But also biotic factors are important ecosystem parameters for succession. For example, the presence of tall competitive plant species is likely to slow down succession for several years because, due to the high cover of litter, phanerophyte species have no opportunity to germinate (Krause 1974, Tilman 1987, Schreiber 2002). This has been a subject of great interest in forest ecology (Bolte 1999). In contrast, the impact of herbivores is considered to induce regressional trends against successional development (Gibson & Brown 1992).

For inland sand ecosystems succession is often observed to be accompanied by a ruderalisation tendency (Stroh et al. 2002). In this case mid-successional stages are characterised by low phytodiversity and dominance of tall competitive grasses (Veer & Kooijman 1997). But also mid-successional stages characterised by high conservation values are observed, and it is of great interest to analyse the reasons behind the divergent developments in order to arrive at a basis for model prediction.

Nutrients

The question whether the phytomass production of terrestrial systems is limited by nutrients and/or other abiotic factors has been intensively discussed (Aerts & Chapin III 2000). Since sand ecosystems are usually nutrient-poor habitats, nitrogen is often regarded as a limiting factor (Arndt et al. 2004, Storm & Bergmann 2004). But also phosphorus plays an important role, especially in the case of calcareous sands (Kooijman et al. 1998, Wassen et al. 2005). Although the availability of nutrients is known to play an important role for species composition in general (Fridley 2002, de Deyn et al. 2004), the question of the ecological significance of nutrients in early successional stages of sand ecosystems has not yet been answered. Analysis of the impacts of increased atmospheric nitrogen deposition and of increased grazing impact on low-productivity habitats is of particularly great interest, in order

to develop adequate methods of ecosystem management. The observed ruderalisation tendency and the decrease of plant species richness is often explained by these factors (Veer 1997, Veer & Kooijman 1997, Kooijman et al. 1998, Matson et al. 2002, Bakker 2005).

Productivity and phytodiversity

Successional pathways as well as an increased nutrient supply are closely associated with an increase in productivity. From the viewpoint of nature conservation, a high diversity of site-specific plant species is characterised by high conservation values, so that the relationship between productivity and species richness is of great interest for ecosystem management.

For the whole ecological gradient many shapes of response curves describing the productivity-diversity relationship have so far been proposed, as reviewed by Mittelbach et al. (2001). Depending on the system, positive (Pfisterer et al. 2004), negative (Goldberg & Miller 1990, Gough et al. 2000) and most often hump-shaped relationships as first proposed by Grime (1973) and Al Mufti et al. (1977) were predominant. Still, no universally valid relationship has yet been detected.

Since sand ecosystems are well known to be low-productivity habitat complexes with a high diversity of site-specific and endangered plant species, and as a decrease of plant species richness connected to nutrient intakes and to a ruderalised successional pathway is observed there, a negative correlation between productivity and diversity can be hypothesised. Further experiments are necessary in order to elucidate the diversity-productivity relationship for sandy grassland habitats.

Grazing

Extensive grazing has turned out to be an important management tool for low-productivity habitats in recent studies (Kooijman & van der Meulen 1996, Provoost et al. 2002, Stroh et al. 2002, Hellström et al. 2003). The effects by which livestock influences the environment are numerous and depend on the ecosystem, grazing intensity and herbivore species (Olff & Ritchie 1998, Gough & Grace 1998). Moderate grazing is beneficial to annual species, whereas ungrazed grassland is dominated by tall perennials and grasses (Noy-Meir et al. 1989). Species richness increases with increasing grazing pressure compared with no grazing, but decreases sharply when the grazing pressure is severe (Olsvig-Whitaker et al. 1993, Mwendera et al. 1997, Taddese et al. 2002).

Probably the most obvious and most important grazing effect is the selective phytomass extraction by herbivores. Thus some plant species or certain plant functional types are

supported, others are discriminated against by a grazing impact, depending on the preferences of the livestock species (Sternberg et al. 2000, Hülber et al. 2005). Nutrients are extracted by phytomass reduction and recycled by elimination from the grazing animal. Therefore, a distribution pattern of nutrients can evolve owing to a grazing impact. Also other factors such as a decrease of litter (Naeth et al. 1991) or an increasing litter turnover by trampling (Ruess & Mc Naughton 1987) are parts of a grazing impact. Hence livestock can have direct and indirect effects on nutrient fluxes (Frank & Evans 1992, Bakker et al. 2003). Additionally, grazing animals influence their environment when they create gaps by trampling, scratching or rolling (Lamoot et al. 2004). These microsites are extremely important for mid-successional ecosystem-types because they represent spots of a regression against succession and regeneration niches for low-competitive plant species, often therophytes which are dependent on patches of bare ground (Bullock et al. 1994, Bakker 2003). In total, the creation of a mosaic of patches is one of the most important mechanisms by which herbivores affect ecosystems (Bakker 2003).

Another important effect is the influence of grazing animals as vectors of diaspores by epi- and endozoogenic transport, which has been intensively discussed by Eichberg et al. (2005) & Eichberg et al. (accepted) for the investigated ecosystem.

For the management of dry and nutrient-poor sand ecosystems, mainly sheep grazing is used as a measure of nature conservation. The effectiveness of sheep grazing as a tool of protection and restoration has been proved in various studies (Stroh et al. 2002, Hellström et al. 2003, Schwabe & Kratochwil 2004, Schwabe et al. 2004). For the management of ruderalised areas with grass-encroachment a more intensive reduction of dominant grasses and an intensive gap-creation can be necessary. We hypothesised that grazing by equids could be an adequate management method and chose donkeys, which are - due to the African origin of the domestic donkey in hot and arid semi-deserts - used to dryness and to living on the scarce vegetation of sand ecosystems (Beja-Pereira et al. 2004, Lamoot et al. 2005a). With respect to traditional land-use also the combination of both livestock species in a multi-species approach is likely to be a suitable management method. Very recently the combination of ruminants and equids has been the focus of attention for nature conservation management in coastal sand ecosystems or wet habitats as well (Menard et al. 2002, Loucougaray et al. 2004, Lamoot et al. 2005b).

Objectives and outline of the thesis

An important first task of this thesis was to develop a model for the successional pathways of sand ecosystems and to elucidate the occurrence of ruderal mid-successional stages with

grass-encroachment on the one hand and species-rich non-ruderalised plots on the other hand. Therefore, long-term studies of sand ecosystems with spontaneous succession in the surroundings of Darmstadt were integrated into a model with a side-by-side comparison of ruderalised and non-ruderalised plots where abiotic factors were analysed. As a result, a successional model which explains different successional pathways of sand ecosystems has been evolved; this is presented in **Chapter 2**.

Based on the results of the successional model, four experiments were carried out to study ecosystem functioning and adequate management methods. Study site was the nature protection area "Ehemaliger August-Euler-Flugplatz von Darmstadt", located in the northern Upper Rhine Valley of Germany. This area served as a model for dry inland sand ecosystems where grazing is used as a management tool. The context incorporating the successional model, the four experiments and the chapters of this thesis is displayed in Figure 1.1, where the focussed themes of each chapter are demonstrated.

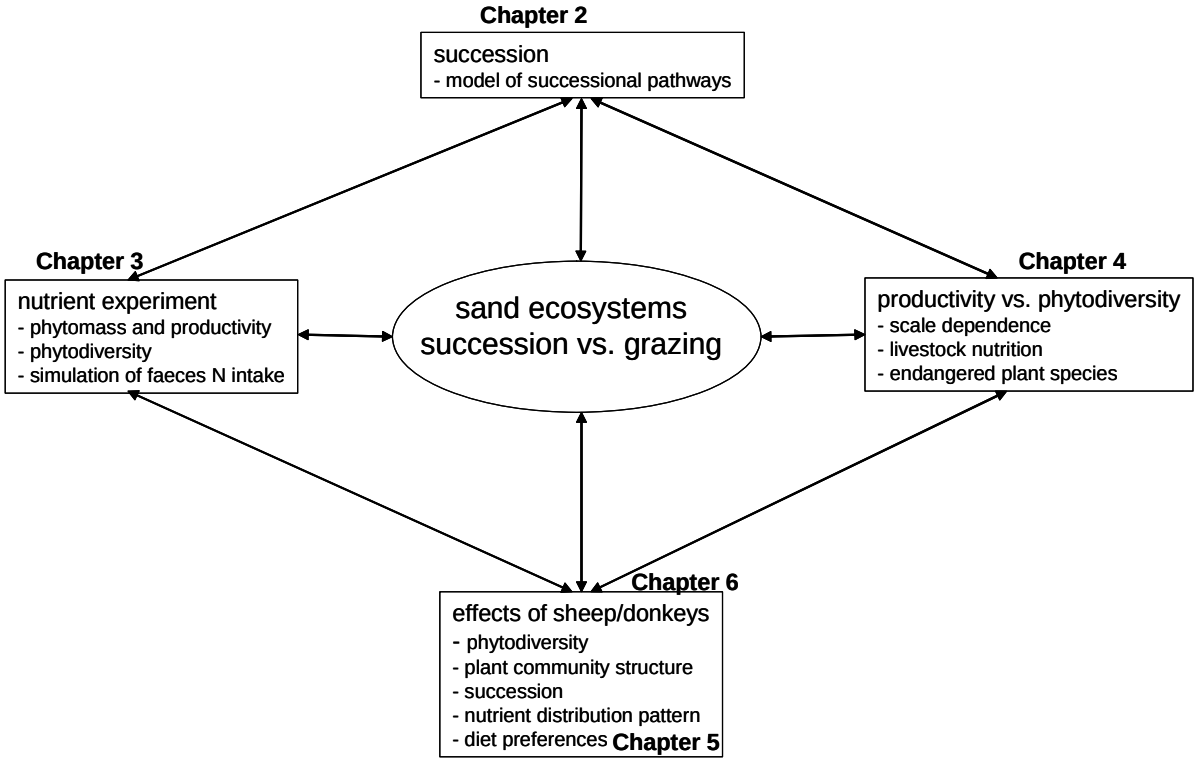

Figure 1.1: Interrelationship between the objectives of this thesis.

To test the successional model by an experimental approach and to analyse limiting factors of sand ecosystems as well as to simulate faeces accumulation sites resulting from grazing, the influences of nutrient addition on the vegetation of sand ecosystems were investigated and are described in **Chapter 3**. Here, the influences of different nutrient treatments on phytodiversity, community structure, phytomass, vegetation structure and on the individual plant, analysed within a four-year experiment, are presented.

The model of successional pathways is also connected to phytodiversity because the described pathways represent a species-rich, non-ruderalised path and a species-poor, ruderalised path. The relationship between plant species richness and phytomass production, i.e. between diversity and productivity, has often been investigated by means of experimental plant communities. But there are some disadvantages: for example, an intact species pool is not guaranteed or species diversity is limited due to plot sizes. The relationship between diversity and productivity was studied within a three-year experiment carried out along a vegetational gradient of sand ecosystems reflecting natural communities. To investigate whether the relationship is scale-dependent, the study was run on fine-grain and on broad scale, with the interrelationship of GIS-based aerial CIR-photos, vegetation data and phytomass analyses. The results of this study are presented in **Chapter 4**. As discussed above, early successional stages of sand ecosystems depend on a grazing impact. As these systems are low-productivity habitats, it has to be guaranteed that livestock nutrition is sufficient. So **Chapter 4** also elucidates the productivity-diversity relationship from the viewpoint of animal nutrition, to demonstrate which sites are the most important ones for nature conservation values as well as for animal nutrition.

With reference to these investigations, a grazing experiment was carried out to analyse the impact of different grazing regimes on the vegetation of sand ecosystems. As a result, it should be concluded which treatment is best suited for the management of low-productivity habitats and as a measure for preventing ruderal pathways of succession with grass-encroachment and low phytodiversity. Sheep grazing, donkey grazing and sheep followed by donkey grazing were compared within a four-year experiment.

In **Chapter 5** the focus is on the foraging behaviour of the different livestock species, and the diet preferences and phytomass extractions associated with each of the three treatments were investigated in a quantitative and in a qualitative phytomass approach.

But besides selective phytomass extraction, grazing impact is also expressed, e.g., by gap creation or eliminative behaviour of the animal species. The effects of the three investigated

treatments on the vegetation were analysed within the scope of an intensive vegetation analysis of grazed areas accompanied by an analysis of special sites and of nitrogen intake at faeces accumulation sites. The results of this study are presented and discussed in **Chapter 6**. A synoptic discussion of the results of all studies is provided in **Chapter 7.**

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Chapter 2:
Succession in inland sand ecosystems: which factors determine the occurrence of the tall grass species *Calamagrostis epigejos* and *Stipa capillata* ?

Abstract

In many successional series, grass species play an important role in mid-successional stages. Using calcareous sand ecosystems in the northern upper Rhine valley (Germany) as a model, we analyse successional trajectories and the factors that determine their direction.

A 5- to 7-year study of 23 permanent plots is presented. The polar ordination revealed that succession starts with pioneer communities (dominated by *Corynephorus canescens* and cryptogams) and can eventually lead to relatively stable *Calamagrostis epigejos* or *Stipa capillata* tall grass stands. At some sites *Cynodon dactylon* can play a major role, but we focused on the two previously mentioned species.

Gradient analyses of their ecological amplitudes by means of principal components and regression analysis were carried out in order to elucidate the factors determining the successional trajectories. Soil analyses of 71 plots established significantly positive linear relations for *C. epigejos* with respect to total nitrogen, extractable phosphate and potassium as well as soil-moisture indicator values. *C. epigejos* is not able to spread if the stress factors nutrient deficiency and dryness are combined. Lower tolerance limits are presented.

In contrast, *S. capillata* shows negative relations to phosphate, declining strongly at P contents > 20 mg * kg^{-1}. At a moisture indicator value of around 3.2 (indicating dry sites) *S. capillata* reaches its optimum. *S. capillata* is a model for a tall grass species which, even with low nutrient levels and dry soil conditions, can be successful in mid-successional phases. But it is displaced by *C. epigejos* if soil moisture increases or phosphate/potassium supply is higher.

Regarding a general framework, the successional phases are characterised by processes such as replacement of species, facilitation and inhibition.

Introduction

According to the information compiled, e.g., by Rebele & Lehmann (2001) and Jentsch & Beyschlag (2003), succession in inland sand ecosystems begins with pioneer communities (often characterised by short grasses such as *Corynephorus canescens* and then passes through a phase of dense sward (often with dominance of tall grasses: "grass-encroachment" in the sense of Kooijman & van der Meulen 1996). Little is known about the details of long-term succession, but according to our observations – as in other systems – the undisturbed succession may be free from shrubs and trees for decades, if persistent grasses are present (Krause 1974, Tilman 1987, Schreiber 2002).

While some information about early and mid-successional phases is available for acidic sandy soils (Jentsch & Beyschlag 2003), less is known about succession on primarily calcareous sand. Especially under subcontinental climatic conditions; permanent plot studies are lacking. Initial observations in our study area showed that especially two grass species can be dominant: *Calamagrostis epigejos* and *Stipa capillata* – sometimes they co-exist, sometimes not.

C. epigejos is of particular interest since its abundance has increased in many regions of Central Europe during recent decades (Rebele 1996, Dormann 1997, Conert 1998, Schwabe et al. 2000). Atmospheric N-deposition (and in general eutrophication) has been identified as one presumable cause (Veer 1997, Veer & Kooijman 1997, Kooijman et al. 1998). The release of formerly agricultural land, which lies fallow now, also favoured *C. epigejos* (Dormann 1997, Rebele & Lehmann 2001). Dominance stands of *C. epigejos* are often characterised by low phytodiversity (Kooijman & van der Meulen 1996, Felinks 2000, Süss 2002, Zehm 2003) and contain few threatened plant species. This is undesirable from the nature conservation point of view (Dormann 1997, Veer & Kooijman 1997, Süss 2002).

In contrast, *S. capillata* is a species with high nature conservation value and decreasing occurrence (Red List species of Germany) and is therefore of considerable interest, as well. It is characteristic of the plant community Allio-Stipetum capillatae; in this plant community even dominance stands of *S. capillata* are of high nature conservation value.

The determining factors for the diverging directions of succession are not obvious. According to Gleeson & Tilman (1990) and Olff et al. (1993) an increase in total soil nitrogen and a decrease of light penetration to the surface during succession on nutrient-poor sandy soils can be recognised. Generally, "a change from a community, governed by the dynamics of colonisation, to one governed by competition for resources" (Chapin III et al. 2002) can be assumed. In the pioneer stages colonisation abilities and stress resistance (against nutrient

deficiency, drought) are important traits for plants, whereas in the mid-successional phases competitive abilities (for light, nutrients) gain in importance (Gleeson & Tilman 1990, Olff et al. 1993).

Nitrogen (N) is often regarded as a key factor in succession (Olff et al. 1993, Chapin III et al. 2002). In the case of calcareous sand, co-limitation of both nitrogen and phosphorus (P) may occur due to the low solubility of calcium phosphate (Kooijman et al. 1998). Additionally, there are indications that in some ecosystems N limitation has been overcome by atmospheric N deposition (Morecroft et al. 1994, ten Harkel & van der Meulen 1996). Potassium (K) is rarely a limiting nutrient in terrestrial temperate ecosystems (Aerts & Chapin 2000), especially in coastal vegetation (Veer & Kooijman 1997), but can be important in wet grassland (Verhoeven et al. 1996). However, we do not know much about its role in inland sand ecosystems. Since sand ecosystems are dry habitats in periods of low precipitation, soil moisture also has to be taken into account as a limiting factor.

While the transition of pioneer communities to dense grassland stages can probably be ascribed to these general principles, it is unclear which factors are decisive for the dominance of different grass species in mid successional stages.

The present study was confined to dry grassland habitats of neutro- and basiphytic (primarily calcareous) inland sand vegetation in the northern upper Rhine valley. We do not consider acidic habitats (see Jentsch & Beyschlag 2003) or *Pinus sylvestris* woodland with understorey of *C. epigejos* (see e.g. Bolte 1999).

In the following we attempt to answer the questions:

1. Successional trajectories: How does succession in these sand ecosystems proceed? Which species dominate in pioneer communities and which in mid-successional stages? What is the position of *C. epigejos* and *S. capillata*?

2. Determining factors: Which soil factors (N, P, K, moisture) correlate with the occurrence of *C. epigejos* and *S. capillata*? What is the shape of their response curves? How can their ecological amplitudes be described? Which factors are likely to determine the occurrence of the species? Can succession be predicted if these factors are known?

Materials and methods

While the questions listed under 1 were examined by a permanent plot study (5-7 years) and community (indirect) ordination, the analysis of the determining factors was addressed by gradient analysis using direct ordination and regression techniques.

The study area

All sample sites are located in the northern upper Rhine valley (8°39''east/49°53''north; districts Darmstadt and Darmstadt-Dieburg) in Hesse/Germany, some 30 kilometres south of Frankfurt/Main. The occurrence of such sandy habitats can be explained by the late glacial to early postglacial aeolian transport of calcareous sand from glacial Rhine deposits. In the course of succession, decalcification took place (Ambos & Kandler 1987). In later postglacial periods, aeolian processes were favoured by anthropo-zoogenic (especially military) impact. Large areas of the sand habitats have been used for military purposes since the Middle Ages, causing disturbances which were followed by successional processes. Today, the most important areas are listed as "Nature Protection Areas" and as "Flora-Fauna-Habitat (FFH)" areas.

The temperature of the study area is characterised by considerable annual fluctuation (about 17.5 °C) and a mean annual temperature of about 9 °C. Given the rather low mean annual precipitation of about 700 mm (Walter & Lieth 1967), intensified by the edaphically extreme sandy sites, the habitats are characterised by warm and dry summers. The annual bulk nitrogen deposition according to our measurements is around 9 kg * ha^{-1} * a^{-1}(Bergmann 2004).

The region belongs to the biogeographical transition zone between subcontinental, subatlantic and submediterranean influence. Therefore, (sub)continental species (e.g., *S. capillata, Bassia laniflora, Koeleria glauca*), suboceanic species (e.g., *Corynephorus canescens*) as well as submediterranean species (e.g., *Silene conica*) occur (Schwabe et al. 2000). Extraordinary plant communities are, above all, the Jurineo-Koelerietum glaucae and the Allio-Stipetum capillatae, which are both restricted to base-rich stands and belong to the priority habitats of the "Flora-Fauna-Habitat" directive (European Union).

The investigated species

Both species in focus are tall perennial C3 grass-species which are able to build up dominance stands. They can produce deep root systems with considerable density in the upper soil: *C.*

epigejos up to 2 m (Conert 1998), *S. capillata* up to 2.8 m (on Chernozem; Kullmann 1957). Thus, the water acquisition capability of both species is excellent.

The distribution of C. *epigejos* (without subsp. *capensis*) is mainly temperate(boreal)-eurasiatic. It is described as a species with very broad ecological amplitudes regarding pH (1.9-8.5 in KCl), soil humus content, soil nutrients (poor sandy soils – fens/fertilised forest floor/ruderal habitats) and soil moisture (wet to dry, provided sufficient water in spring) (Werner 1983, Ellenberg 1996, Rebele 1996, Rebele & Lehmann 2001).

S. capillata has a mainly (sub-)continental-eurasiatic distribution (Oberdorfer 2001, Rebele & Lehmann 2001) and is restricted to neutral-alkaline, dry and nutrient-poor soils (Conert 1998, Oberdorfer 2001). According to the detailed investigations of Rychnovská and Úlehlová (1975) in former Czechoslovakia, *S. capillata* is – as confirmed by our measurements – a neutro- to basiphytic species (pH average 90 samples: KCl 6.2, H_2O 7.4).

The propagation ability of *S. capillata* even over distances (Rychnovská & Úlehlová 1975) is well known. In the core region of its distribution, the species therefore has a "ruderal" tendency. *S. capillata* is able to become established on anthropogenic habitats, even on abandoned fields, but can sustain itself only if there are periods of desiccation (Ellenberg 1996).

Vegetation and soil analyses

Each year, vegetation was recorded on 23 permanent plots (not managed, each mainly 25 m^2) over 5 or 7 vegetation periods (1995/1997 to 2001) with the cover/abundance scale of Barkman et al. (1964). Nomenclature of the vascular plants follows Wisskirchen & Haeupler (1998), for the bryophytes Koperski et al. (2000) and for the lichens Scholz (2000).

Additionally, 71 plots (not managed) of the same vegetation complex as the permanent plots (often adjacent) were selected in 2001 (each 30 m²). Vegetation was recorded as described above. In each of these plots, 16 systematically arranged soil samples were taken with a Pürckhauer soil corer in July 2001. The samples were bulked to two composite samples of 8 samples each. The upper soil (0-10 cm depth) and lower soil horizon (10-30 cm) were sampled separately. Samples were kept cool to prevent microbial nitrogen mineralisation. After 24 hours at most they were sieved (2 mm) and frozen (-18 °C) until extraction. Calcium chloride extracts (0.0125 mol * l^{-1}) were prepared to assess extractable nitrate and ammonium and calcium acetate/calcium lactate extracts (CAL) for phosphorus and potassium (VDLUFA 1991). Analyses were carried out photometrically with a Skalar SAN except for potassium, which was analysed by atomic absorption spectrometry. pH-values were measured in 0.01

mol * l^{-1} calcium chloride suspension. Total nitrogen content was determined with a N-analyser (Carlo Erba 1400) after drying and grinding. Accuracy was ascertained by certified material (soil standard 1 provided by Hekatech, Germany, 100.9 % of certified value, n =7). All soil data given below refer to dry (105 °C) soil. Average values for the two composite samples from each plot are given.

It was not possible to measure the water content of all plots simultaneously or continuously. Therefore, soil moisture was calculated by means of Ellenberg indicator values (Ellenberg et al. 1992). The average value of all species present in each plot was taken. Schaffers & Sýkora (2000) showed that these moisture indicator values are a very valuable tool for site calibration. They discovered a significant correlation with lowest soil moisture contents in summer of r = 0.84.

Additionally, at each plot, the percentage of flowering *C. epigejos* shoots was assessed and the two lowest leaves of 16 shoots were sampled. These were dried, ground and analysed regarding the nitrogen content like the soil samples.

Ordinations and statistical analyses

An ordination of the vegetation data was performed with polar ordination (= Bray-Curtis ordination) by means of PC-ORD, 4.25. The cover/abundance scale was transformed into a cover scale beforehand. The selected options were: Sørensen measure of similarity, variance regression as endpoint selection, Euclidean axis projection. Even though some ecologists ignore polar ordination, it proved to be a valuable tool in many comparative studies (recent compilation in McCune & Grace 2002). Especially the variance regression endpoint selection eliminates any subjectivity and ignores outliers. In our case, detrended correspondence analysis produced essentially the same results. Correspondence analysis was severely influenced by outliers.

A principal components analysis (PCA) was carried out on the correlation matrix of the soil data with PC-ORD. While PCA is not an appropriate ordination method for vegetation data with long gradients (in our case: 5.7 SD), it is one of the most effective methods to reduce the dimensionality of environmental data with high degree of inter-correlation (Beals 1984, Kent & Coker 1992, McCune & Grace 2002). The use of the correlation matrix, which centres and standardizes the data matrix, is necessary since the variables have unequal scales.

Correlation and logistic regression analyses were done with SAS 8.02, multiple regressions with EXCEL.

Results

Indirect ordination: Successional trajectories

Figure 2.1 shows the results of the Polar Ordination of the 23 permanent plots (triangles) over 5-7 years of spontaneous succession. The diagram shows a continuum with four separated branches and a broad centre. Table 2.1 gives the mean cover of the dominant species (> 5 % cover) of each branch and the centre in order to elucidate the vegetation composition. Apart from cryptogams, grass species are the most prominent species in all branches:

- I. Open sand vegetation rich in cryptogams. Amongst phanerogams, *Corynephorus canescens* reaches the highest mean cover. (Pearson's correlation coefficient with first axis r_1 = -0.27) (Bromo-Phleetum arenarii, Corynephoretalia basal community and Koelerion glaucae). These are pioneer stages.
- II. Stands with predominance of *S. capillata* (Allio-Stipetum) (Pearson's correlation coefficient with second axis r_2 = 0.52).
- III. Dominance stands of *C. epigejos* (Pearson's correlation coefficient with first axis r_1 = 0.82)
- IV. Stands with predominance of *Cynodon dactylon* (Pearson's correlation coefficient with first and second axis r_1 = -0.31, r_2 = -0.35) and the moss *Hypnum lacunosum*.

The centre is characterised by co-existence of the branch species and in some cases by dominance of the medium-sized grass species *Elymus repens*, *Poa angustifolia*, or *Bromus tectorum*.

Seven permanent plots with clear successional direction have been connected by trajectories. In the other cases, the trajectories were fluctuating or short and are omitted for clarity of the diagram. Of special interest are the plots 3 and 7 which document how successional trajectories beginning in the centre can lead to different branches by increase of the respective grass species.

In the 2, 5 or 4 cases where the starting point lay within branch number 2, 3 or 4, respectively, the trajectory remained within the branch, indicating a relative stability once a branch is reached.

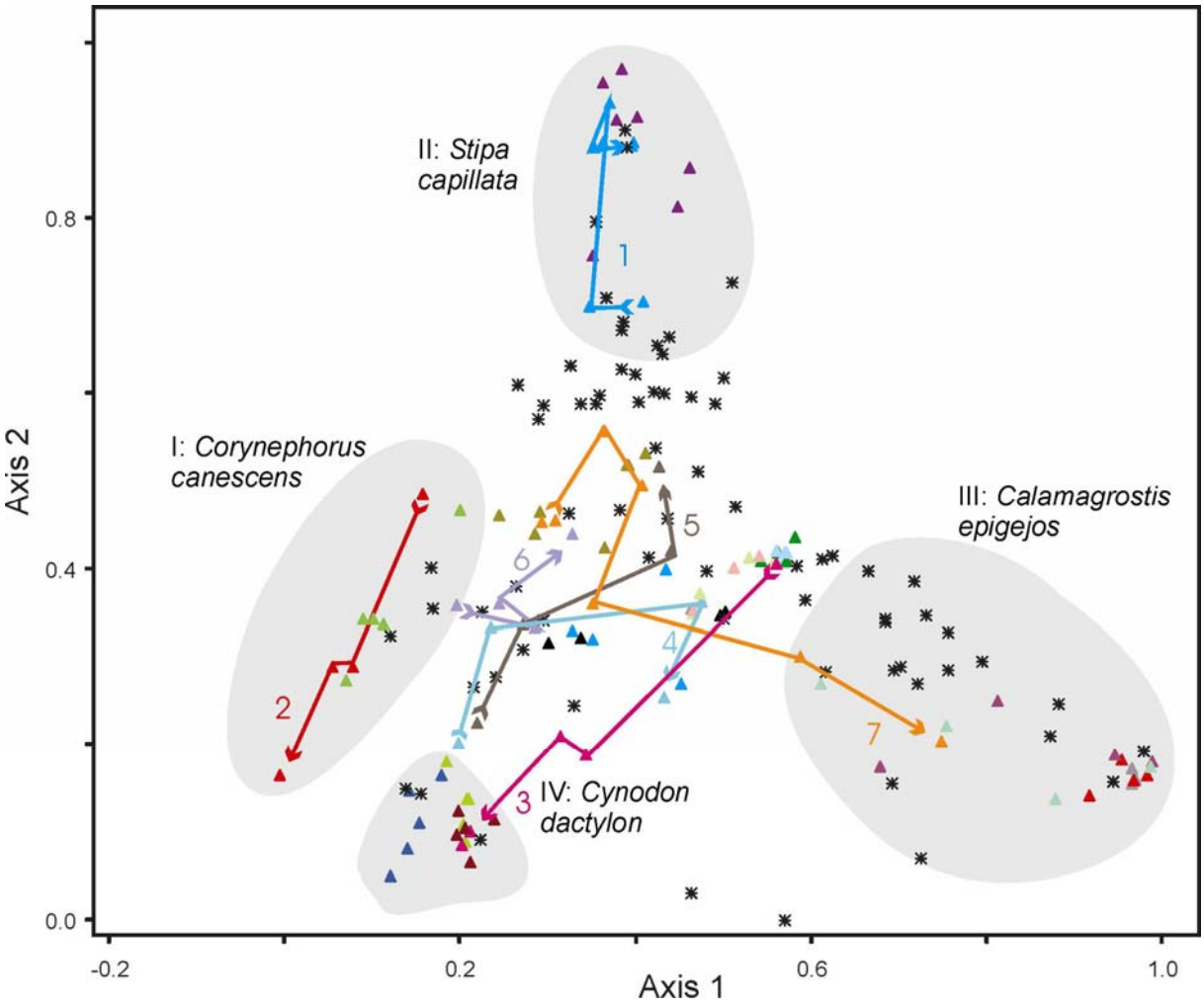


Figure 2.1. Polar ordination diagram of the species composition of all plots. Triangles: permanent plots with 5 to 7 years spontaneous succession. Successive years of each plot are connected by time trajectory vectors, if there was a clear direction (5 years: plots 2, 3, 4, 5 and 6; 7 years: plots 1, 7). Otherwise, triangles in the same plot that represent different years are printed in the same colour, but are not connected. Asterisks: plots with soil analyses. The branches I-IV (highlighted in grey) are explained in the text and Table 2.1. Axis 1 extracted 14.9 % of the original distance matrix, axis 2 another 13.5 %.

Thus the diagram suggests that succession begins with pioneer stages, passes through a transition zone (centre) and can then take one of three directions, leading to mid-successional stages with dominance of the mentioned grass species. The position of *S. capillata* and *C. epigejos* is clearly separated; they represent different successional directions. We have no indication of a conversion between these branches. The C4-invader *Cynodon dactylon* is not yet present at all sites due to lack of dispersal and was therefore not included in the following gradient analyses.

Branch I		**Branch II**	
(B) *Hypnum lacunosum*	40.4 (4.0)	(G) *Stipa capillata*	19.8 (3.8)
(B) *Tortula ruraliformis*	13.4 (4.2)	(G) *Festuca duvalii/ovina* agg.	11.1 (1.7)
(L) *Cladonia rangiformis/furcata* /spec.	13.0 (4.2)	(B) *Tortula ruraliformis*	7.9 (3.6)
(G) *Corynephorus canescens*	9.8 (2.9)	(H) *Helianthemum nummularium*	6.2 (1.2)
(L) *Peltigera rufescens*	6.3 (1.8)		
(G) *Festuca duvalii/ovina* agg.	6.2 (3.0)	**Branch III**	
(G) *Bromus tectorum*	5.2 (2.8)	(G) *Calamagrostis epigejos*	57.5 (4.2)
		(G) *Poa angustifolia*	15.2 (2.3)
		(B) *Brachythecium albicans/rutabulum*	8.2 (3.4)
		(B) *Hypnum lacunosum*	6.0 (1.6)
Centre		**Branch IV**	
(G) *Poa angustifolia*	13.4 (1.9)	(B) *Hypnum lacunosum*	78.8 (2.7)
(B) *Hypnum lacunosum*	13.2 (1.9)	(G) *Cynodon dactylon*	37.7 (6.1)
(G) *Elymus repens*	11.8 (3.0)	(G) *Poa angustifolia*	19.8 (4.3)
(B) *Tortula ruraliformis*	11.0 (2.4)	(H) *Sedum acre*	6.3 (2.1)
(G) *Bromus tectorum*	8.3 (1.5)	(G) *Carex praecox*	5.6 (2.7)

Table 2.1. Vegetation composition of the branches and the centre in Figure 2.1. Mean cover values are given for those species which exceed 5 % (standard error of the mean in parenthesis). G: grass species (Poaceae and *Carex*), H: herbs, B: Bryophytes, L: Lichens.

With the help of the permanent plot data we are able to determine the successional status of the 71 nutrient ecological sampling plots (indicated as asterisks). They are situated especially in the *S. capillata-C. epigejos* transition zone and are therefore well suited for the investigation of the site conditions of the mid-successional phase.

Soil characteristics

The results of the soil analyses of the 71 sites are shown in Table 2.2. The soil consists of sand with only minor fractions of silt and clay. Gravel and stones are also negligible. The pH values of the upper soil samples range from 5.3 to 7.5 but only at three sites (nos. 54, 55, 60) is the pH below 7. Total nitrogen content ranges from 0.26-1.9 g * kg^{-1}, mineral nitrogen ($CaCl_2$ extract) content from 0.6-7.9 mg * kg^{-1}, phosphate-P (CAL extract) from 3-152 mg * kg^{-1}. The distribution of this element is very skewed. Potassium is also characterised by huge differences, but the distribution is more symmetrical. In our data set, Ellenberg's indicator values of soil moisture (amplitude for terrestrial plant species: 1-9; 1 = extremely dry; 9 = wet sites) cover a small span of 2.6-4.4 (dry to weakly moist sites).

	pH_u	pH_l	Nt_u	Nt_l	Nmin_u	Nmin_l	P_u	P_l	K_u	K_l	moisture
minimum	5.28	6.13	0.26	0.05	0.64	0.14	2.5	0.6	18.1	9.2	2.58
25 % quartile	7.23	7.26	0.51	0.18	1.95	0.70	6.7	5.3	33.8	21.8	3.25
mean	**7.23**	**7.33**	**0.76**	**0.28**	**2.65**	**0.89**	**29.3**	**24.9**	**50.2**	**38.4**	**3.44**
median	**7.30**	**7.38**	**0.65**	**0.29**	**2.65**	**0.89**	**9.8**	**7.7**	**42.7**	**33.1**	**3.42**
75 % quartile	7.37	7.45	0.92	0.37	3.55	1.26	45.0	27.1	59.4	43.7	3.65
maximum	7.53	7.61	1.90	0.66	7.94	4.04	152.0	152.8	146.5	145.8	4.44
standard deviation	0.36	0.25	0.33	0.12	2.18	0.61	36.4	36.6	26.7	27.8	0.35

Table 2.2. Soil characteristics of the plots (n = 71). _u : upper soil (0-10 cm), _l : lower soil (10-30 cm).

Correlations between soil parameters

Table 2.3 shows many inter-correlations between soil parameters. There are highly positive correlations between phosphorus and potassium (r = 0.59 in the upper, r = 0.75 in the lower soil horizon). The correlations between total nitrogen and mineral nitrogen are also conspicuous (r = 0.53 in the upper horizon). Each parameter is correlated between upper and lower soil horizon. The correlations between moisture indicator value and most nutrient contents are only weak (r around + 0.3). Due to the high degree of inter-correlations, a PCA should help to reduce data complexity.

	pH_u	pH_l	Nt_u	Nt_l	Nmin_u	Nmin_l	P_u	P_l	K_u	K_l	moisture
pH_u	1.00										
pH_l	**0.93**	1.00									
Nt_u	-0.21	-0.13	1.00								
Nt_l	**-0.26**	-0.23	**0.35**	1.00							
Nmin_u	0.05	0.02	**0.53**	0.12	1.00						
Nmin_l	0.09	0.07	-0.03	0.13	**0.39**	1.00					
P_u	0.04	-0.05	**-0.27**	**0.25**	0.09	**0.32**	1.00				
P_l	0.03	-0.05	**-0.25**	**0.32**	0.08	**0.27**	**0.97**	1.00			
K_u	-0.11	-0.18	-0.06	**0.31**	-0.02	-0.01	**0.59**	**0.64**	1.00		
K_l	-0.09	-0.17	-0.23	**0.35**	-0.16	0.05	**0.70**	**0.75**	**0.90**	1.00	
moisture	**-0.26**	**-0.32**	0.16	**0.42**	**0.27**	**0.29**	**0.30**	**0.30**	**0.35**	**0.30**	1.00

Table 2.3. Pearson's correlation coefficients of the soil variables (n = 71). _u: upper soil (0-10 cm), _l: lower soil (10-30 cm). Significant correlations ($p < 0.05$) are shown in bold print.

Principal components analysis of the soil parameters

Figure 2.2 depicts the ordination of the sites along the PCA axes. The first axis of the principal components analysis extracted 41 % of the variance. This axis is highly correlated with both phosphorus and potassium contents of the soil (Table 2.4). Many plots with high scores on the first axis have been used formerly as arable land (nos. 1-6, 99, 100, 128, 130), some as orchards (78-87, 126), or are influenced by debris deposits (119).

The second axis, which extracted another 22 % of the variance, is correlated with total nitrogen and mineral nitrogen, especially in the upper horizon (Table 2.4). On the third axis two stands (nos. 6, 126) with high mineral nitrogen content in the lower horizon are separated

from the rest. This axis, as well as the following ones, is not readily interpretable in ecological terms.

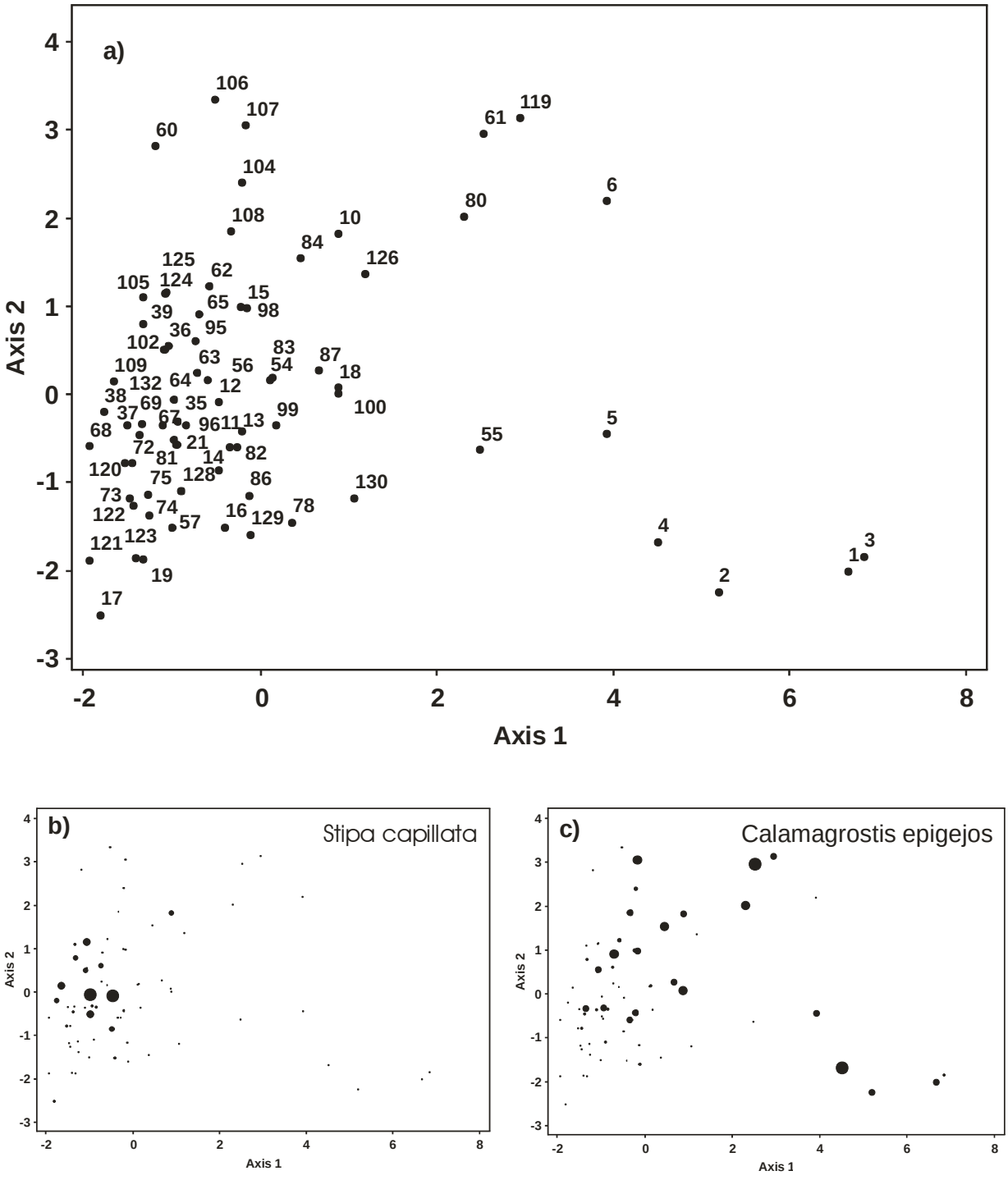


Figure 2.2. (a) Principal components analysis (PCA) of the soil variables of 71 stands. (b)-(c): Overlays with plant species cover: the sizes of the plot symbols are proportional to the relative size of the respective species *S. capillata* (b) and *C. epigejos* (c).

	I	II	III
Nt (upper soil)	-0.14	**0.79**	0.42
Nt (lower soil)	0.48	0.44	0.42
Nmin (upper soil)	0.10	**0.80**	-0.27
Nmin (lower soil)	0.31	0.41	**-0.71**
P (upper soil)	**0.88**	-0.13	-0.29
P (lower soil)	**0.91**	-0.13	-0.21
K (upper soil)	**0.81**	-0.12	0.35
K (lower soil)	**0.88**	-0.26	0.25
moisture	0.53	0.46	0.08

Table 2.4. Pearson's correlation coefficients of the principal component axes I-III with the soil variables.

The moisture indicator value shows weak correlations with the first and second axes. According to Figure 2.2, this is based on a group of sites characterised by low values in the lower left hand corner of the diagram.

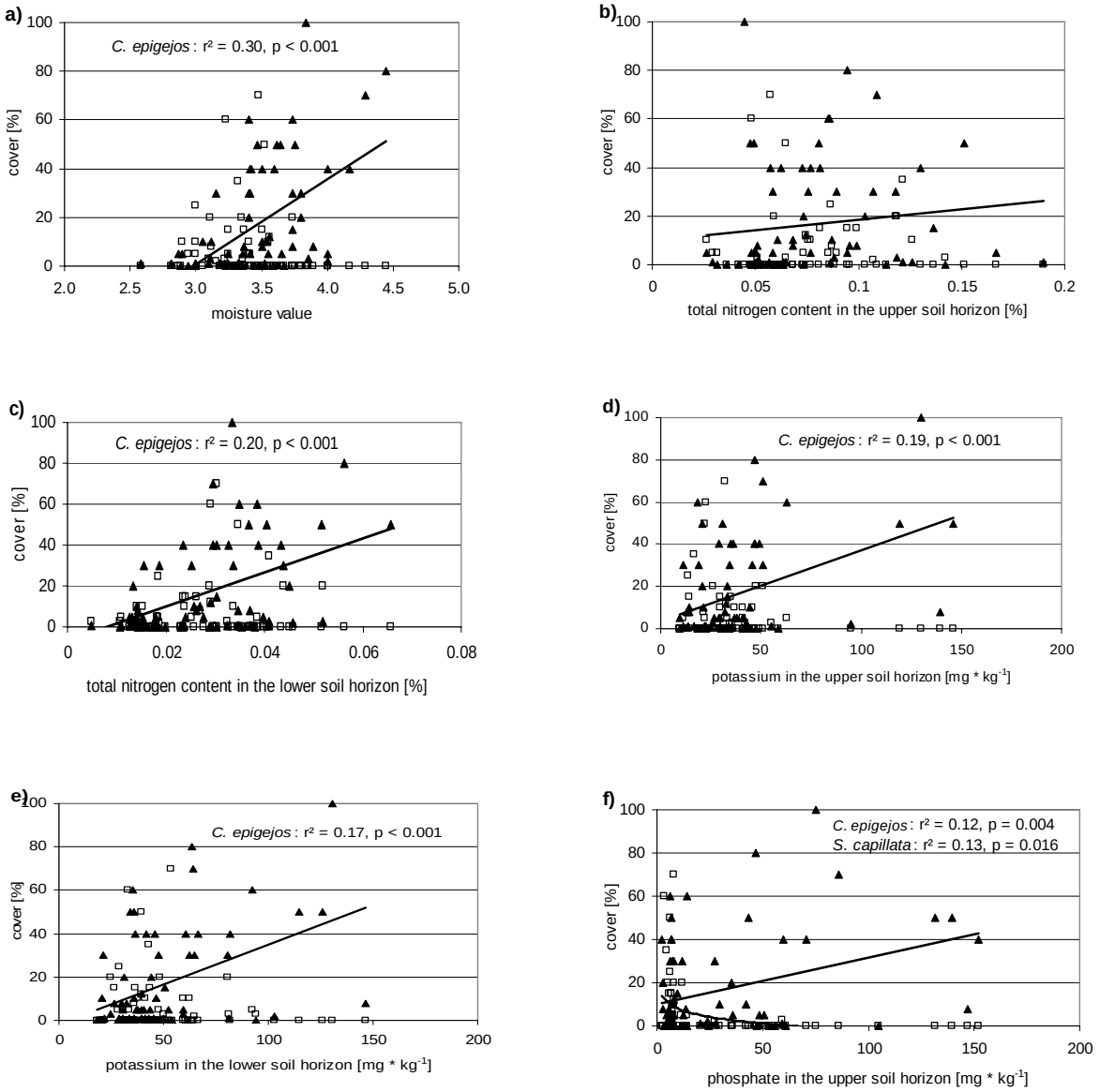
The cover percentages of *S. capillata* and *C. epigejos* at each plot are visualised by the symbol size in Figures 2.2b and c. *S. capillata* only occurs at low values of the first axis (sometimes decreasing at very low values) and mostly at moderate values of the second. Both response curves are unimodal. In contrast, *C. epigejos* has a monotonic response curve and thrives best at moderate to high values of the first axis (r = 0.50). The correlation to the second axis is weak (r = 0.25) since high and low cover percentages occur at each section of the gradient. There are some stands on which both grass species are present but only with rather low cover values of these species.

Regression of C. epigejos *on soil parameters*

Univariate analyses show significant positive linear relations between cover of *C. epigejos* and moisture indicator value (Figure 2.3a), total nitrogen in the lower soil horizon (Figure 2.3c) and potassium as well as phosphorus in both horizons (Figures 2.3d-g). The species did not cover more than 5 % of the ground if one of the following limits was reached: moisture value < 3; N_t(upper soil) < 0.42 g * kg^{-1}; N_t(lower soil) < 0.13 g * kg^{-1}; K(upper soil) < 19.6 mg * kg^{-1}; K(lower soil) < 9.6 mg * kg^{-1}; N_{min}(lower soil) < 0.53 mg * kg^{-1}. At 41 sites, we found *C. epigejos* with cover percentages of 5 % or below. 22 of these sites fall short of the above-mentioned limits; another 5 sites are adjacent to permanent plots with increasing cover values of *C. epigejos* or might not include this species due to lack of dispersal.

Multiple regression produced the model described in Table 2.5. The adjusted coefficient of determination reaches $r^2 = 0.37$. N_t(lower soil), K(upper soil) and moisture indicator value were selected as independent variables. Nearly the same coefficient of determination resulted from a multiple regression using the PCA scores of the axes I, II and V as independent variables. The mean nitrogen content of the *C. epigejos* leaves was 1.8 %. No correlation with

the cover percentage nor with soil nitrogen content was apparent. The percentage of flowering sprouts of *C. epigejos* significantly correlates with the P content of the soil ($r^2 = 0.31$) and the cover value ($r^2 = 0.36$). Both factors together result in an adjusted coefficient of determination of $r^2 = 0.46$. Whereas in stands of up to 20 mg * kg^{-1} P at most 50 % of the sprouts come to flower, the percentage of flowering sprouts rises as high as 90 % in case of higher P values.



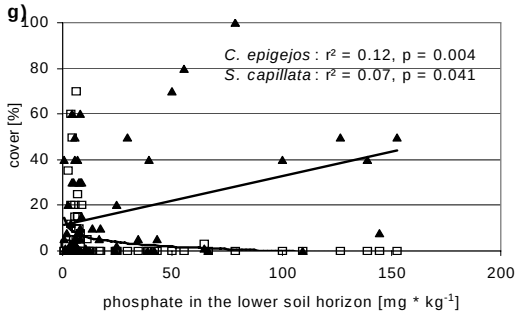


Figure 2.3. Regressions of the cover of *C. epigejos* (filled triangles) and *S. capillata* (quadrangles) on soil variables. (a) Ellenberg's moisture indicator value, (b) total nitrogen in the upper soil, (c) total nitrogen in the lower soil, (d) extractable potassium in the upper soil, (e) extractable potassium in the lower soil, (f) extractable phosphorus in the upper soil, (g) extractable phosphorus in the lower soil.

Regression of S. capillata on soil parameters

S. capillata was absent at 63 % of the sites, the soil of which was analysed. Simple linear (or curvilinear) regression of cover percentages did not lead to significant models due to the many zero values stated in the data set, except for negative logarithmic curves on phosphate (Figures 2.3f-g). Thus, we applied logistic regression for modelling the probability of occurrence of *S. capillata*. Only two factors were significant (Figure 2.4):

1. Phosphate (negative relation):

Phosphorus seems to set a clear upper limit for the occurrence of *S. capillata*: while *S. capillata* was found at 56 % of the sites with P(upper soil) < 15 mg * kg^{-1} (n = 43), it was present at only 7 % when P(upper soil) was > 20 mg * kg^{-1} (n = 28) (no stands with 15 mg * kg^{-1} < P < 20 mg * kg^{-1} occurred in our data set).

2. Moisture indicator value (optimum curve):

The response curve towards the moisture indicator value shows an optimum at about 3.2, which indicates dry sites. At values < 2.5 and > 3.8, the probability of occurrence was nearly 0. This is a narrow amplitude.

Both factors could be included in a multiple logistic regression model (Table 2.5).

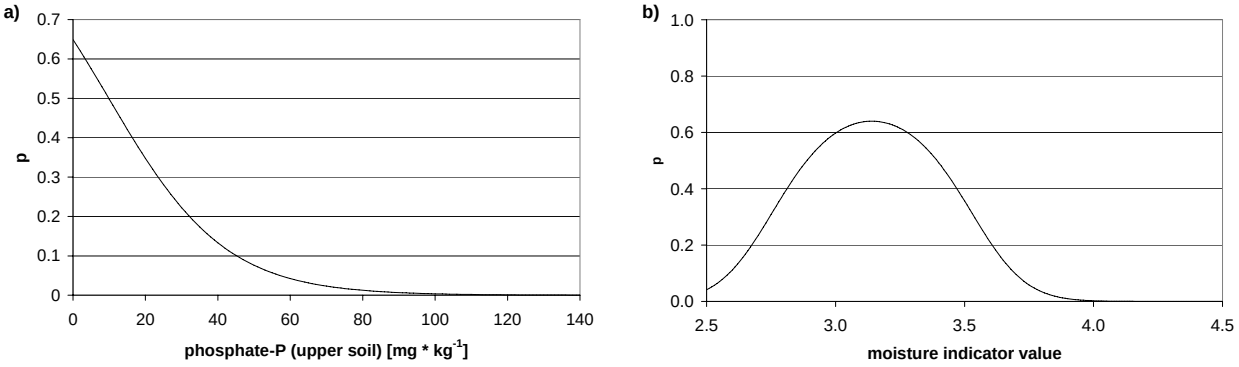


Figure 2.4. Logistic regressions of the occurrence probability (p) of *S. capillata* on soil variables. (a) phosphorus (CAL extractable), (b) Ellenberg's moisture indicator value.

	b	S.E. of b	p
Calamagrostis epigejos			
intercept a	-75.89	19.6	0.0003
Nt (lower soil)	434.44	196.67	0.0307
K (upper soil)	0.21	0.09	0.0199
moisture	20.26	6.27	0.0019
Stipa capillata			
intercept	104.5	44.59	0.0190
P (upper soil)	0.07	0.03	0.0038
moisture	-67.35	27.48	0.0143
moisture²	10.65	4.21	0.0115

Table 2.5. Regression parameters for multiple linear regression of *C. epigejos* ($r^2_{adjusted} = 0.37$, $p < 0.0001$) and multiple logistic regression of *S. capillata* (likelihood ratio chi² = 35.75; p = 0.0001; -2 log L = 57.54), S.E.: standard error.

Correlation between S. capillata and C. epigejos

To examine the relations between the two species we used Spearman's rank correlation coefficient. Only the 26 stands with presence of *S. capillata* or *C. epigejos* were included, to prevent undue influence of too many zero values. The rank correlation coefficient amounts to -0.56, indicating a significant negative relation (p = 0.003) between the two species.

Discussion

Successional trajectories

The results concerning the course of succession in our system (Figure 2.1) correspond to some general principles such as:

- The replacement of species (Egler 1954): First, mainly seed/spore-bank species like *Corynephorus canescens*, therophytic dicots and the moss *Tortula ruraliformis* occur. Later, there is an increase of the cover of tall grass species (especially *S. capillata, C. epigejos*), which are not abundant in the seed bank (for seed-bank data see Thompson et al. 1997, Krolupper & Schwabe 1998, Jentsch & Beyschlag 2003). We have not detected these species in the seed rain so far (Krolupper & Schwabe 1998, Stroh et al. 2002), but have recorded, in permanent plots, new settlements of both species based on generative dispersal. The cover percentages of *S. capillata* and *C. epigejos* increase with the decrease of raw soil.
- Humus content and nitrogen mineralisation increase in the course of successional processes (Storm et al. 1998) by production of litter, allowing species other than raw-soil pioneers to thrive. These aspects correspond to the principle of "facilitation" (Connell & Slatyer 1977, Leuschner & Rode 1999, Leuschner & Gerlach 2000).
- Especially in the case of *C. epigejos* (together with the development of a thick litter layer and strong light absorbance), the establishment of tall grass species leads to inhibition

(Connell & Slatyer 1977) of the typical endangered early colonists, e.g. *Medicago minima* and *Helichrysum arenarium*.

Soil characteristics

The soils are very homogeneous regarding pH. pH probably does not exert any decisive influence on the studied vegetation stands.

Total nitrogen content can be considered to be low or even very low compared to the range of meadows and pastures (0.6-6.2 g * kg^{-1}, Scheffer & Schachtschabel 2002), but lies within the span typical for sand ecosystems (Bornkamm 1977, Tilman 1986, Wurbs & Glemnitz 1997). Mineral nitrogen (mostly as nitrate in our case) is provided by mineralisation, which in turn is dependent on the amount of mineralizable organic material, as indicated by total nitrogen. This explains the positive correlation between the two. In sand ecosystems, there is also a close correlation between humus and nitrogen contents (Tilman 1987, Storm et al. 1998). Both are enriched in the soil during the course of succession (Tilman 1986, Gleeson & Tilman 1990, van Rheenen et al. 1995, Storm et al. 1998, Aerts & Chapin 2000).

The distribution of CAL-extractable phosphorus is very wide and skewed. On the one hand, Scheffer & Schachtschabel (2002) state that in the case of values above 40-50 mg * kg^{-1} there is no further yield increase on arable land. Thus, there is a considerable P accumulation at some sites. On the other hand, values below 10 mg * kg^{-1} are low, but typical for sand dunes (Berger-Landefeldt & Sukopp 1965). Contents below 15-20 mg * kg^{-1} can be regarded as natural in the soils of the study area (Storm et al 1998). Higher contents are most probably caused by former use as arable land with application of fertilisers or some other anthropogenic source of eutrophication. Other studies have shown that especially phosphate contents (and to a lesser extent potassium) do not rapidly decrease after cessation of fertilisation – in contrast to nitrogen (Marrs et al. 1991). Thus we arrive at the conclusion that P (and K) indicate man-made eutrophication. These nutrients are not related to any successional processes from sand pioneer communities to grassland (Storm et al. 1998). It is argued that they prevent the establishment of semi-natural vegetation (Marrs et al. 1991, Aerts et al. 1995, Willems & van Nieuwstadt 1996). In concentrations of more than 50 mg * kg^{-1}, potassium is not considered to be a limiting nutrient in agriculture (Scheffer & Schachtschabel 2002). Again, we can conclude that some plots are overly supplied with potassium while on others the contents are low.

Principal components and regression analysis

The first axis of the PCA ordination of the environmental variables is closely connected with potassium and phosphorus. According to the above statements, this is a P (and K) eutrophication axis. The second axis correlates with total and mineral nitrogen as spontaneous succession indicators. This corresponds to the appearance of early successional species at lower values of this axis.

The PCA reveals that *C. epigejos* and *S. capillata* occupy different positions along the environmental gradients. The amplitude of *C. epigejos* is relatively wide. However, this species appears neither on those plots that are characterised by extremely low values on the first axis, nor on most plots marked by low values on the second axis (pioneer stages). This means that *C. epigejos* only occurs in mid-successional stages and above all in P/K enriched habitats such as former fields. In accordance with the PCA, significant linear regression curves on the nutrients N on the one hand and P and K on the other hand as well as on soil moisture could be observed.

The relation of *S. capillata* to soil parameters is quite different. According to the ordination diagram in Figure 2.2, *S. capillata* attains high cover values only in a relatively small amplitude: low values of the first axis (P, K eutrophication) and moderate values of the second axis (nitrogen – succession). In contrast to *C. epigejos*, low cover values of *S. capillata* even occur on some pioneer plots.

The question remains to be discussed, whether the mentioned correlations with soil factors are likely to be the result of causal relationships. We will discuss possible reasons for the observed amplitude separation on the basis of evidence in the literature in the following paragraphs.

C. epigejos

In principle, positive coincidences of soil nutrients and plant cover percentage always raise the question of cause and effect. An intensive colonisation by grass, establishing a more important above-ground phytomass, might surely cause humus accumulation which then, above all in the case of sandy soils, will improve the nutrient availability. Wedin & Tilman (1990) proved that the characteristics (e.g. nitrogen mineralisation) of originally identical soils can be changed by the influence of different grass species. However, Collins & Wein (1998) showed different successional events on neighbouring, experimentally fertilised sites. Evidence for the facilitation of *C. epigejos* growth by nutrient supply (especially N and P) has been established experimentally in several studies (Boot & den Dubbelden 1990, Bornkamm

et al. 1993, Brünn et al. 1996, Rebele 1996, Brünn 1999, Lammerts et al. 1999). In our case, direct effects of P (but not N or K) on *C. epigejos* are suggested by the correlation with flowering rate. These results might lead to the conclusion that in fact, due to nutrient deficiency, *C. epigejos* in some cases cannot establish high coverage percentages, and that the growth will physiologically be promoted by succession (N) and by man-made eutrophication (P + K). In our examinations, the effects of K and P cannot be separated due to their strong inter-correlation. Positive feedback caused by *C. epigejos* phytomass production can then additionally increase the nutrient contents of the soil. The fact that there is no correlation between coverage and leaf nitrogen contents is not contradictory to this hypothesis of nutrient limitation. Improved nitrogen supply will obviously be used entirely for increased phytomass production. *C. epigejos* can sometimes also become established despite low nutrient supply, but normally does not reach high coverage rates.

Besides the nutrients, water supply obviously also plays an important role. There is a basic correlation between water and nutrient contents, since during the succession, the supply of water as well as nutrients improves. However, as this correlation is not too strong, water obviously plays its own role, a fact that is confirmed by the multiple regression model. Plots with an average moisture indicator value lower than 3.0 usually show no occurrence of *C. epigejos*. There are only a few exceptions, where those plots are sparsely populated by *C. epigejos*. Our permanent plot studies show that, although *C. epigejos* repeatedly tries to establish itself in extremely dry habitats of our region, its colonisation is not successful in the long run; in this case, the species reaches its autecological limits of colonisation.

On one hand, the limiting effects of water can have direct consequences (dryness damage to *C. epigejos* was observed on drifting sands during the extremely dry June 2003). On the other hand, shortage of water can also have indirect consequences due to decreasing nutrient uptake. Thus, Köster (1974) could show that P-absorption on sandy soils correlates with precipitation. Conversely, the water use efficiency of *C. epigejos* increases with nitrogen fertilisation (Boot & den Dubbelden 1990). It is generally known that nutrients can extend the moisture amplitudes (Ellenberg 1996). Our data show that *C. epigejos* does not reach high cover values if the stress factors nutrient deficiency and dryness are combined.

S. capillata

In contrast to *C. epigejos*, this species must thus be able to cope with dry soils. At a moisture indicator value of around 3.2 (dry sites) *S. capillata* even reaches its optimum. Climate diagrams from the global *S. capillata* distribution area show that in the eastern part (Kysyl-

Orda, Aral Sea) there are fully arid periods of about seven months (Rychnovská & Úlehlová 1975). Ecophysiological investigations in the Vinschgau (inner-alpine Festucetalia valesiacae zone) by Florineth (1974) have shown that although *S. capillata* has no effective water saving strategy, it compensates for high transpiration rates by an extensive root system. Thus, *S. capillata* does not suffer as much from water deficits as do other plant species at the same site (Ellenberg 1996). The reduced cover of *S. capillata* in pioneer communities of our data set is most probably not caused by dryness. There are also no clear indications of nutrient limitation. Colonisation dynamics might play a more important role.

Unlike *C. epigejos*, *S. capillata* is absent from relatively nutrient-rich and less dry habitats as well. This is especially true for P, as we found a strong decline at P > 20 mg * kg^{-1}. Total and mineral nitrogen did not play an important role concerning *S. capillata* presence. The occurrence of this grass species is obviously also hampered by moisture indicator values beyond its optimum of 3.2. Nutrients and moderate soil moisture might not suppress *S. capillata* directly, but indirectly via competitors (Ponomarev 1946 cited by Rychnovská & Úlehlová 1975). A superior competitor might be *C. epigejos*, as is suggested by the negative correlation of r_S = -0.56 between the two species.

Comparison of C. epigejos and S. capillata

According to Lichter (2000), successional patterns in sand dunes are "widely explained by a trade-off between plant colonisation and competitive abilities". Our data suggest that the mid-successional stages are determined: 1. by competitive abilities (predominance of *C. epigejos*), 2. by stress resistance (predominance of *S. capillata*). In the case of *C. epigejos*, aut- and synecological amplitudes (fundamental and realised niche) are nearly identical. There are lower limits of moisture and nutrient supply (given in the results section) beyond which the species cannot occur. These characterise *C. epigejos* "resistant" sites. Once these limits are reached, there is a monotonic increase in *C. epigejos* cover.

S. capillata, in contrast, is synecologically displaced to dry and nutrient poor soils and profits from its drought resistance and low nutrient requirements. Yet, there is a transition zone where both species can co-exist with rather low cover values.

The success of tall grass species is generally remarkable. Prach & Pyšek (1999) found in successional series of man-made habitats in the Czech Republic, that the most successful species

in succession are tall, wind-pollinated, capable of intensive lateral spread, and require high nutrient supply and sufficient site moisture. Important elements of the characterisation are

fulfilled mainly by *C. epigejos*, but in stands where nutrient and moisture conditions are not sufficient, this species is replaced by *S. capillata* as another tall grass species. Therefore *C. epigejos* fits in the scheme defined by Prach & Pyšek (1999), whereas *S. capillata* is a model for a tall grass species which is successful at low nutrient and low moisture levels.

On the basis of the response curves presented above it should be possible to derive succession prognosis, e.g. for stands in the centre of Figure 2.1. There is a relatively ordered progression from stades with definable early colonists to specific branches representing differentiated tall grass stades.

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Chapter 3:
How does nutrient addition affect the pioneer grassland vegetation of calcareous inland sand ecosystems?

Abstract

In a 4-year study we examined whether the phytomass production by pioneer stages of inland sand ecosystems is limited by nutrients, and how vegetation is influenced by different nutrient treatments. During 2000-2005 we investigated pioneer grassland (Koelerion glaucae) of the northern Upper Rhine Valley (Germany) on nutrient-poor calcareous sand. The year 2003 was extraordinarily dry and warm. Within a 5-fold replicated randomised block design, 10-m² plots were treated with organic carbon (C), phosphorus (P), nitrogen (low [n] and high dosages [N]), NP, NP+ potassium (NPK) and NPK+ micro- and macronutrients (NPKM) and compared to a control. We studied effects on soil nutrient content, phytomass production, cover of vegetation layers, species composition, diversity, vegetation height and seed production. The results show:

1) A two-fold increase of phanerogam phytomass production after nutrient addition, implying nutrient limitation.

2) A significant increase of the height of 6 species, a tendency towards increase in 11 species, a decrease in 1 species and a significant increase of seed production for 3 species.

3) No change in species composition and phytodiversity.

We conclude that besides nutrients, water is the main limiting factor for the studied plant community. After 4 treatment years, competition has not yet become strong enough for species to outcompete one another; instead, nearly all species benefit from a nutrient input. With nitrogen application, phosphorus becomes limiting. For most variables, the effect of nitrogen or phosphorus alone was not significant, even in high dosage. The combinations NP, NPK and NPKM, on the other hand, did affect the vegetation, indicating a co-limitation of N and P. Accumulation of faeces or urine can lead to an increase of phytomass and ruderalisation, whereas a homogeneous distribution of dung pellets does not influence the vegetation.

Introduction

In dry ecosystems, not only water but also nutrients are often regarded as limiting factors for phytomass production (Arndt et al. 2004, Storm & Bergmann 2004). Thus, the availability of nutrients plays an important role for the species composition (Fridley 2002, de Deyn et al. 2004). Above all, nitrogen is said to be a key factor in succession (Olff et al. 1993, Chapin III et al. 2002). Some other investigations have also pointed out the importance of phosphorus, especially in the case of calcareous sands (Kooijman et al. 1998, Süss et al. 2004a, Wassen et al. 2005). But the question of the ecological significance of nutrients in early successional stages of sand ecosystems has not been answered yet. According to Boeye et al. (1997) in spite of the fact that there are disadvantages, fertilisation experiments are still the most straightforward method for detecting nutrient limitation. As Kahmen et al. (2005) have pointed out, there is a need to study natural ecosystems. Many authors have investigated the effects of fertilisation in grassland communities, especially coastal sand dunes in Great Britain and The Netherlands (e.g. Willis 1963, Atkinson 1973, Boorman & Fuller 1982, Kachi & Hirose 1983, Bobbink 1991, Morecroft et al. 1994, Day 1996), but to our knowledge, no study investigating a calcareous inland sand ecosystem with species-rich pioneer communities exists.

In most experiments, nitrogen increased phytomass production and decreased phytodiversity (Tilman 1987, Elisseou et al. 1995, Day 1996, Unkovich et al. 1996, Jones et al. 2004). Often the phytomass increase was even greater in the case of NP fertilisation, which implies a co-limitation between nitrogen and phosphorus (Davy & Bishop 1984, Bobbink 1991, Morecroft et al. 1994, Chiarucci et al. 1999, Mamolos et al. 2005), while Fabaceae species mainly benefit from phosphorus applied solely (Janssens et al. 1998).

Concerning the plant species composition of temperate grassland, during recent decades a ruderalisation tendency along with a loss of plant species richness has been observed, which is often explained by increasing atmospheric nitrogen depositions or abandonment of agricultural land use (Veer 1997, Veer & Kooijman 1997, Kooijman et al. 1998, Matson et al. 2002, Bakker 2005). According to Török et al. (2000) organic carbon addition (C) is a possible way to immobilise soil nitrogen and thus may be an effective restoration tool.

In our study we concentrate on a grazed sand ecosystem where sheep - and to a smaller degree also donkeys - are used as grazing animals to counteract ruderalisation, grass-encroachment and succession (Süss et al. 2004b). From the viewpoint of nature protection, many important effects are achieved by grazing (Stroh et al. 2002, Schwabe & Kratochwil 2004, Schwabe et al. 2004, Eichberg et al. 2005). But grazing can also lead to an accumulation of nutrients at

urine and faeces spots, especially in the case of equids' grazing. Therefore our experiment also tries to simulate the accumulation of animal excreta and its influences on the vegetation in a grazed ecosystem. According to Brenner et al. (2004) N and P (dung patches) and N, P and K (urine patches) are the elements with strongest input in case of sheep grazing. So we analysed the effects of different nutrient treatments (C, N, P, NP, NPK and NPK + other macro- and micronutrients) on above- and below-ground phytomass as well as on species composition over a 4-year period. Additionally, we investigated the effects on the height and fruiting success of all plant species with sufficient abundance after 4 years of treatment. In brief, we focus on the following questions:

1) Is the phytomass production of inland sand ecosystems limited by nutrients? Which nutrients are decisive?
2) Are the individual plant species limited by nutrients?
3) Does the species composition, cover of plant functional types or phytodiversity change after nutrient addition?
4) Are there any effects of a moderately increased deposition of nitrogen on the vegetation?
5) What are the conclusions for grazed ecosystems regarding faeces accumulation sites?

Materials and Methods

Study area

The investigation took place in the northern Upper Rhine Valley (Germany) about 30 km south of Frankfurt/Main (Hesse) near Darmstadt. The substrate is drifted sand which had been blown-out from calcareous Rhine deposits during late glacial and post-glacial periods. The soil type is a calcaric Arenosol and soil data are given in Table 3.1. Mean annual temperature is about 10.8 °C (data from Frankfurt/Main airport for the period 1991 to 2004 [Internet]) with a mean annual duration of sunshine of 1690 h. Together with the rather low mean annual precipitation rate of about 600 mm $year^{-1}$ these features characterise the dry and warm climate of the region. The vegetation of the study site is composed of plant communities belonging to early successional stages of the Koelerion glaucae vegetation complex. The whole area is grazed by sheep for purposes of conservation.

	mean	SD
NO_3^--N [mg*kg-1]	1.50	1.10
NH_4^+-N [mg*kg-1]	0.78	0.81
PO_4^{3-}-P [mg*kg^{-1}]	11.20	6.10
pH	7.50	0.10
N_{total} [%]	0.51	0.27
$CaCO_3$ [%]	7.50	6.10
C_{org} [%]	4.70	3.20

Table 3.1. Soil data from the investigated area, referring to upper soil (0-10 cm). Four plots were analysed in May and in September of the years 2000 and 2001 (n = 52). Data refer to analyses of Bergmann (2003). SD: Standard deviation.

Weather during the investigated years

Since the first vegetation relevés were sampled in September 2000 and the last in June 2005, the weather data for this period are used as background information (data from Frankfurt/Main airport, Internet). As Table 3.2 demonstrates, the year 2003 was extraordinary due to a higher temperature in summer, a longer duration of sunshine and an extremely low precipitation rate.

	average 1991-2004	2000	2001	2002	2003	2004
temperature [°C]	10.8	11.6	10.8	11.2	11.4	10.7
duration of sunshine [h *a $^{-1}$]	1686	1559	1560	1619	2138	1632
precipitation [mm * a -1]	606	759	753	778	379	556

Table 3.2. Weather during the investigated years 2000 - 2005 in relation to the long-term average of the years 1991-2005. Data from Frankfurt/Main airport.

Experimental design

The experimental design was a randomised block design, five times replicated. The five blocks (V, W, X, Y, Z) were established in an early successional stage of Koelerio-Corynephoretea grassland representing the Sileno conicae-Cerastietum semidecandri (Berg et al. 2004).

The five blocks consisted of eight treatment plots each with a size of 10.24 m². Every treatment plot was divided into a permanent plot of 4 m² where the vegetation was recorded and a surrounding area designated for phytomass and soil sampling. The buffer between the plots was 50 cm. Every block was fenced in order to protect it against grazing sheep and rabbits. Blocks with surrounding *Cynodon dactylon* presence were protected against an invasion of the rhizomatous C4-grass by a plastic shield extending 20 cm into the soil.

Nutrient treatments

The eight different treatments are shown in Table 3.3. Except for the sawdust (which was added once a year), the nutrients were applied dissolved in tap water. Nutrient application occurred 10 times a year in order to keep leaching losses small and to avoid unphysiological nutrient concentrations and scorching due to osmotic stress. The first application took place in June 2001. The annual amount of water added by the experiment is 10 mm (1.7 % of the mean annual precipitation and thus negligible).

The composition of the nutrient solution was the same as the "balanced fertiliser" used by Atkinson (1973) with the following exceptions: NH_4NO_3 and NaH_2PO_4 x 2 H_2O were used instead of $(NH_4)_2HPO_4$ and $(NH_4)_2SO_4$ in order to separate the nutrient elements N and P. K was applied as KCl instead of K_2SO_4 and Mn as $MnSO_4$ x 1 H_2O. N was applied at a low dosage (n) of 25 kg ha^{-1} a^{-1} instead of 83 kg ha^{-1} a^{-1} in order to simulate an increased atmospheric deposition, which is about 17 kg ha^{-1} a^{-1} including wet and dry deposition (Bergmann 2004). The high-dosage N (N) of 100 kg ha^{-1} a^{-1} served as a test for N limitation. The input of organic carbon (as sawdust and saccharose) was as specified by Török et al. (2000) and was intended to stimulate microbial biomass and to reduce the nutrients available for plant uptake.

treatment	element	chemical formula	annual addition kg element * ha^{-1} * a^{-1}
0 (Control)		-	-
C	C	$C_{12}H_{22}O_{11}$	547
	C	sawdust	145
P	P	$NaH_2PO_4*2H_2O$	50
n	N	NH_4NO_3	25
N	N	NH_4NO_3	100
NP	N	NH_4NO_3	100
	P	$NaH_2PO_4*2H_2O$	50
NPK	N	NH_4NO_3	100
	P	$NaH_2PO_4*2H_2O$	50
	K	KCl	60
NPKM	N	NH_4NO_3	100
	P	$NaH_2PO_4*2H_2O$	50
	K	KCl	60
	Mg	$MgSO_4*7H_2O$	52
	Fe	$FeC_6H_5O_7*5H_2O$	13
	B	$Na_2B_4O_7*10H_2O$	2.72
	Mn	$MnSO_4*1H_2O$	13.23
	Zn	$ZnSO_4*7H_2O$	0.23
	Cu	$CuSO_4*5H_2O$	0.25
	Mo	$(NH_4)_6Mo_7O_{24}*4H_2O$	0.54

Table 3.3. Applied nutrients and dosages for the different treatments.

Soil analyses

In 2000 (status quo samples), 2002 and 2004, always in September, soil samples for nutrient analyses were taken at least four weeks after the last nutrient application. At each of the 6 phytomass-sample subplots of each plot, 2 samples of 10 cm depth were taken with a Pürckhauer soil corer. The samples were bulked to two composite samples of 6 samples each and were kept cool to prevent microbial nitrogen mineralisation. After 24 h at most, they were sieved (2 mm) and frozen (-18 °C) until extraction.

Plant-available nitrogen and ammonium were measured in calcium chloride extracts (0.0125 mol l^{-1}), phosphate and potassium in calcium acetate/calcium lactate extracts (CAL) according to VDLUFA (1991). Analyses were carried out photometrically with a Skalar SAN, except for potassium which was analysed by atomic absorption spectrometry. pH values were measured in 0.01 mol l^{-1} calcium chloride suspension. All soil data given below refer to dry (48 h at 105 °C) soil.

Vegetation relevés

Twice a year, in May/June and in September, the vegetation cover of the 40 permanent plots (8 treatments x 5 replicates) was estimated on a percentage scale. Since the first relevés took place in September 2000, the relevés of autumn and the following spring were combined into one annual vegetation relevé by using the maximum values for each plant species. So the combined relevés of 2000/2001 are status quo samples before the nutrient treatment started. The nomenclature of the vascular plants follows Wisskirchen & Haeupler (1998), those of the bryophytes Koperski et al. (2000) and those of the lichens Scholz (2000).

The cover of different vegetation layers was analysed by addition of all maximum values of all plant species in the respective layer. For the analysis of the mean cover values of certain species, the absence of a species for each plot was counted as “0 %” only if the species was present at least once during the investigation years, as a proof of its presence in the species pool of the plot. For the analysis of species composition, the total species number, number of the plant functional types “graminoids”, “herbs”, “bryophytes”, “lichens”, “graminoids + herbs” and “bryophytes + lichens” and the ruderalisation index according to Stroh et al. (2002) were analysed.

Phytomass

Every year in September the phytomass was sampled. For each treatment plot, 6 subplots of 20 cm x 20 cm size were chosen at random, clipped to ground and the above-ground

phytomass separated into the plant functional types “graminoids and herbs”, “Fabaceae” and “cryptogams”, bulked together for each plot. Additionally, the litter was sampled. At every plot below-ground phytomass up to a soil depth of 30 cm was sampled with a corer 4.7 cm in diameter and sieved with a mesh width of 0.71 mm. The phytomass was dried for 48 h at 70 °C and afterwards weighed. Above-ground phytomass reaches maximum values in the studied vegetation type in September, as was revealed by vegetation structure analysis based on digital image processing (Zehm 2003). Thus, these peak standing crop data can serve as rough estimates of net primary productivity. Even though this method underestimates primary production (as simultaneous growth and death are not accounted for, see Long et al. [1989]) it is commonly used (e.g. Bonser & Reader 1995, Allock & Hik 2003, Osem et al. 2004).

Species height

In 2004 in May and in September, the height of 19 plant species with sufficient frequency on the plots was measured at each plot by taking the average value of ten randomly chosen individuals per plot and per species. The species were: *Arenaria serpyllifolia* agg., *Bromus tectorum, Carex hirta, Centaurea stoebe, Corynephorus canescens, Cynodon dactylon, Echium vulgare, Erodium cicutarium* agg., *Euphorbia cyparissias, Helichrysum arenarium, Medicago minima, Phleum arenarium, Psyllium arenarium, Salsola kali* ssp. *tragus, Saxifraga tridactylites, Sedum acre, Senecio vernalis, Setaria viridis* and *Silene conica.*

Seed production

Also in 2004, the number of produced seeds per individual was counted for the species *Bromus tectorum, Centaurea stoebe, Erodium cicutarium* agg., *Euphorbia cyparissias, Sedum acre* and *Silene conica*. At each plot, ten randomly chosen individuals were examined - each plant species at its peak of fruiting on the control plots. All the 40 plots were examined on the same day.

Statistical analyses

Plant species composition was analysed by means of detrended correspondence analysis using PC Ord 4. The analysis was run with downweighting and rescaling, the number of segments was 26, the percentage cover data were used without transformation.

To analyse the effects of the variables “treatment” and “year” on the dependent variables, mixed linear models were calculated (SAS 8.02, Proc Mixed), which are especially suitable for analysing repeated-measures data (Littell et al. 1998) because they allow comparison of

the goodness of fit of several covariance structures. We tested autoregressive (1), heterogeneous autoregressive (1), autoregressive moving averages (1,1), unstructured, compound symmetry and Huynh-Feldt and chose the one with the best Akaike (AIC) values for the final calculations. First of all, the status quo values from the year 2000 (in case of the vegetation data the combined relevé of September 2000 and May 2001) were analysed separately to look for initial differences between the plots. Afterwards the 4 treatment years were analysed together. If the interaction term "treatment*year" was significant, the four years were then analysed separately to allow a Dunnett-adjusted analysis between the seven treatments in comparison to the control group. If more than one treatment was significant, Tukey-adjustment was used to test for differences between these treatments. Significance was set at a level of $p < 0.05$.

Results

Soil analyses

Figure 3.1 shows the nutrient contents and the pH values of the soil (0-10 cm depth) in the years 2000, 2002 and 2004. There are no significant differences between the plots in 2000, before the experimental treatment started.

As the result of the mixed-linear-models analyses show (Table 3.4), mineral nitrogen content and potassium contents are influenced by the treatment, while for phosphorus the significant term "treatment*year" demonstrates an increasing accumulation. The pH values are dependent on the year but not on the treatment.

The mineral nitrogen content is hardly influenced by the treatments: only in the case of the N treatment is a significant increase of 1.4 times detectable. All plots treated with phosphorus (P, NP, NPK, NPKM) show significantly higher phosphorus contents in the soil in 2002 and even more in 2004. After 4 years (2004) the phosphorus content is about five times higher at the P-treated plots than in the control, whereas in 2002, when only phosphorus was applied (P), the result was significantly higher phosphorus contents than in the case of NPK or NPKM addition (Tukey-adjustment).

A 2.0-fold increase of the applied nutrient can also be observed in the case of potassium; the soil samples of the plots NPK and NPKM have significantly higher potassium contents than the control group.

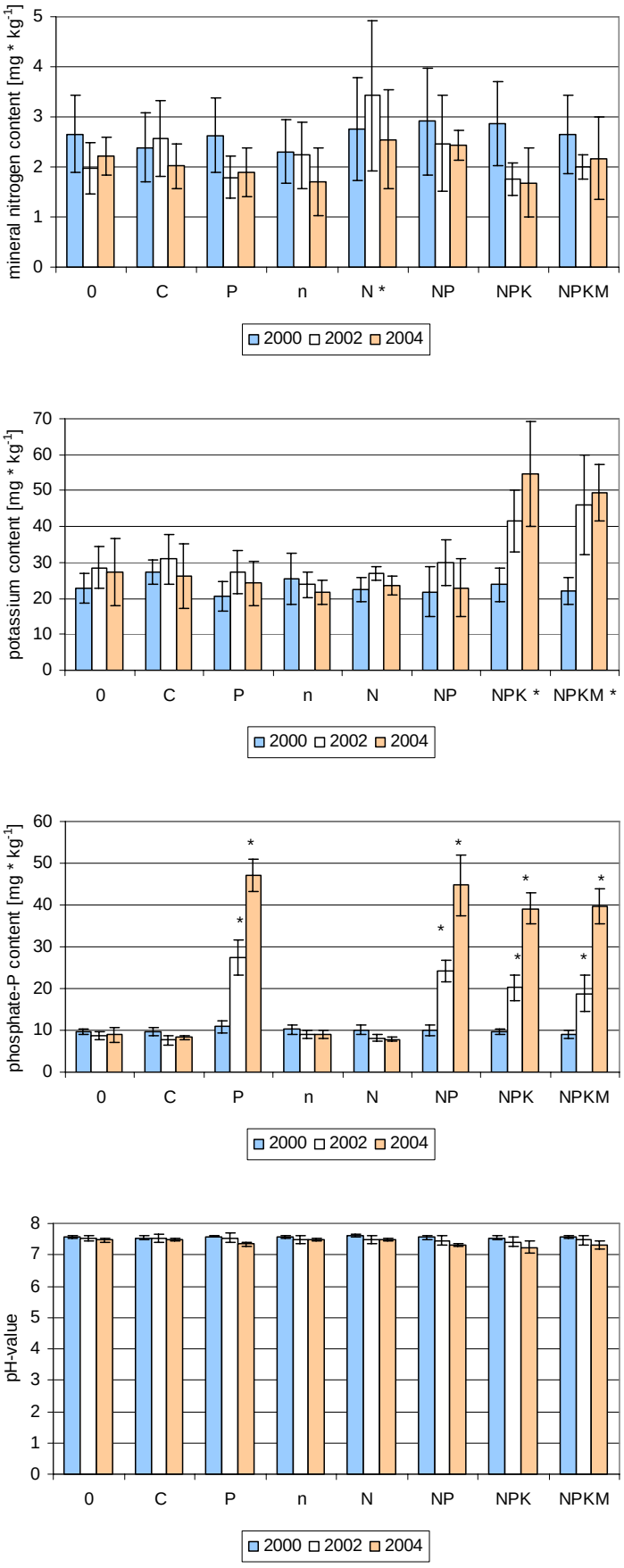

Figure 3.1. Nutrient contents and pH-values of the treatment plots for the years 2000, 2002 and 2004. Treatment effects that are significantly different from the control for effect years (2002, 2004) are marked with an "*****" at the inscription of the x-axis. Effects that are significant for a certain year are marked with an "*****" over the bar of the concerned year. Error: Mean absolute deviation from the mean.

Effect	Num df	Den df	F-Value	p	Effect	Num df	Den df	F-Value	p
Nmin					**Potassium**				
treatment	7	26.9	3.25	**0.0124**	treatment	7	28	17.02	**<0.0001**
year	1	32	0.25	0.5586	year	1	32	0.05	0.8248
treatment*year	7	32	1.13	0.3714	treatment*year	7	32	2.02	0.0836
Phosphate-P					**pH**				
treatment	7	28	91.69	**<0.0001**	treatment	7	10.2	1.97	0.1579
year	1	32	230.63	**<0.0001**	year	1	32	13.68	**0.0008**
treatment*year	7	32	32.18	**<0.0001**	treatment*year	7	32	1.03	0.4303

Table 3.4. Results of the mixed linear models of mineral nitrogen content (Nmin), phosphorus and potassium contents and pH values of the soil. Significant results are shown in bold print. Num df: degrees of freedom numerator, Den df: degrees of freedom denominator, p: level of significance.

Phytomass

The phytomass of “graminoids and herbs”, “cryptogams” and “roots” as well as “litter” was not significantly different between the plots before the treatments started. But within the analyses of the 4 treatment years, all analysed variables show a highly significant effect of the year ($p<0.0001$, Table 3.5). Above-ground phanerogam phytomass production on the control plots was lowest in 2003 (55 g * m^{-2}) and highest in 2001 (131 g * m^{-2}), which means that there were annual fluctuations by a factor of 2.4. To allow a better comparison of the treatment effect, Figure 3.2 represents the different amounts of phytomass with the control set at 100 % for each year.

No significant interaction “treatment*year” is discernible. The factor “treatment” is significant for the variable “graminoids and herbs”, the phytomass of which is about twice as high in the case of N, NP, NPK or NPKM addition as in the control. In the case of the cryptogams, the treatment effect is only almost significant and only a tendency for an increased cryptogam phytomass in case of C addition and a decrease with NPKM treatment can be observed. “Fabaceae” were only sparsely present, so their phytomass could not be analysed statistically.

Effect	Num df	Den df	F-Value	p	Effect	Num df	Den df	F-Value	p
graminoids and herbs					**cryptogams**				
treatment	7	53.6	11.6	**<0.0001**	treatment	7	23.4	2.41	0.0520
year	3	48.4	10.6	**<0.0001**	year	3	96	32.29	**<0.0001**
treatment*year	21	48.4	1.33	0.2018	treatment*year	21	96	1.4	0.1379
roots					**litter**				
treatment	7	28.4	1.09	0.4133	treatment	7	43.7	1.96	0.0832
year	3	94.8	8.21	**<0.0001**	year	3	42.3	14.29	**<0.0001**
treatment*year	21	94.8	0.89	0.6077	treatment*year	21	42.3	1.41	0.1687

Table 3.5. Results of the mixed linear models of the phytomass of different plant functional types and litter. Significant results are shown in bold print. Num df: degrees of freedom numerator, Den df: degrees of freedom denominator, p: level of significance.

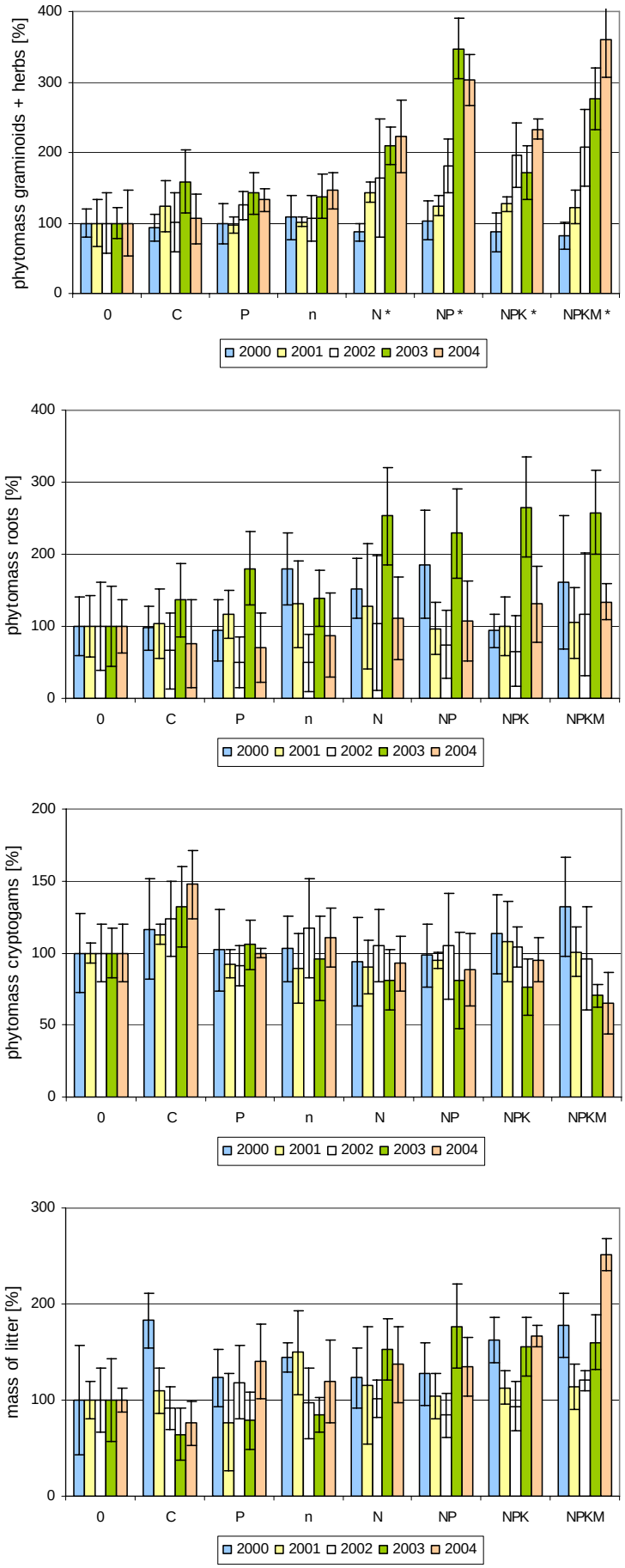

Figure 3.2. Phytomass of different plant functional types and litter. Treatment effects that are significantly different from the control for effect years (2001-2004) are marked with an "*****" at the inscription of the x-axis. Error: Mean absolute deviation from the mean. The phytomass of the control is set at 100 % for each year. Absolute values [g * m^{-2}] for 100 % are a) graminoids and herbs. 2000: 89; 2001: 131; 2002: 70; 2003: 55; 2004: 75. b) roots. 2000: 297; 2001: 580; 2002: 767; 2003: 223; 2004: 423. c) cryptogams. 2000: 447; 2001: 725; 2002: 573; 2003: 477; 2004: 596. d) litter. 2000: 31; 2001: 30; 2002: 63; 2003: 31; 2004: 29.

Cover of vegetation layers and individual plant species

Like the phytomass samples, the covers of the different layers of vegetation were not initially different. Analysing the 4 treatment years, the factor "year" is highly significant for all investigated strata (see Table 3.6). The cover percentages decreased in 2002/2003 for all treatments; thus, as for the phytomass analyses, Figure 3.3 depicts the cover values in relation to the control group to allow a better comparison of the treatment effects.

As the interaction term "treatment*year" is not significant for any of the plant functional types, only the treatment effects are considered. The graminoid layer is significantly affected by the treatment with NPKM-addition. Its cover is nearly doubled in comparison to the control group, as shown in Figure 3.3. For herbs, this effect is even stronger (2 - 2.5-fold increase) and is significant for the treatments NP, NPK and NPKM. For bryophytes and lichens, no significant treatment effect is detectable.

Effect	Num df	Den df	F-Value	p	Effect	Num df	Den df	F-Value	p
graminoids					**lichens**				
treatment	7	37.7	4.85	**0.0006**	treatment	7	26.5	0.36	0.9164
year	3	51	17.26	**<0.0001**	year	3	42.2	17.55	**<0.0001**
treatment*year	21	51	0.39	0.9897	treatment*year	21	42.2	0.57	0.9180
herbs					**total**				
treatment	7	25.8	8.39	**<0.0001**	treatment	7	33.7	7.33	**<0.0001**
year	3	32	33.29	**<0.0001**	year	3	57	19.21	**<0.0001**
treatment*year	21	32	1.08	0.4112	treatment*year	21	57	0.82	0.6803
bryophytes									
treatment	7	38.4	1.61	0.1600					
year	3	96	68.69	**<0.0001**					
treatment*year	21	96	1.33	0.1775					

Table 3.6. Results of the mixed linear models of the cover of different vegetation layers. Significant results are shown in bold print. Num df: degrees of freedom numerator, Den df: degrees of freedom denominator, p: level of significance.

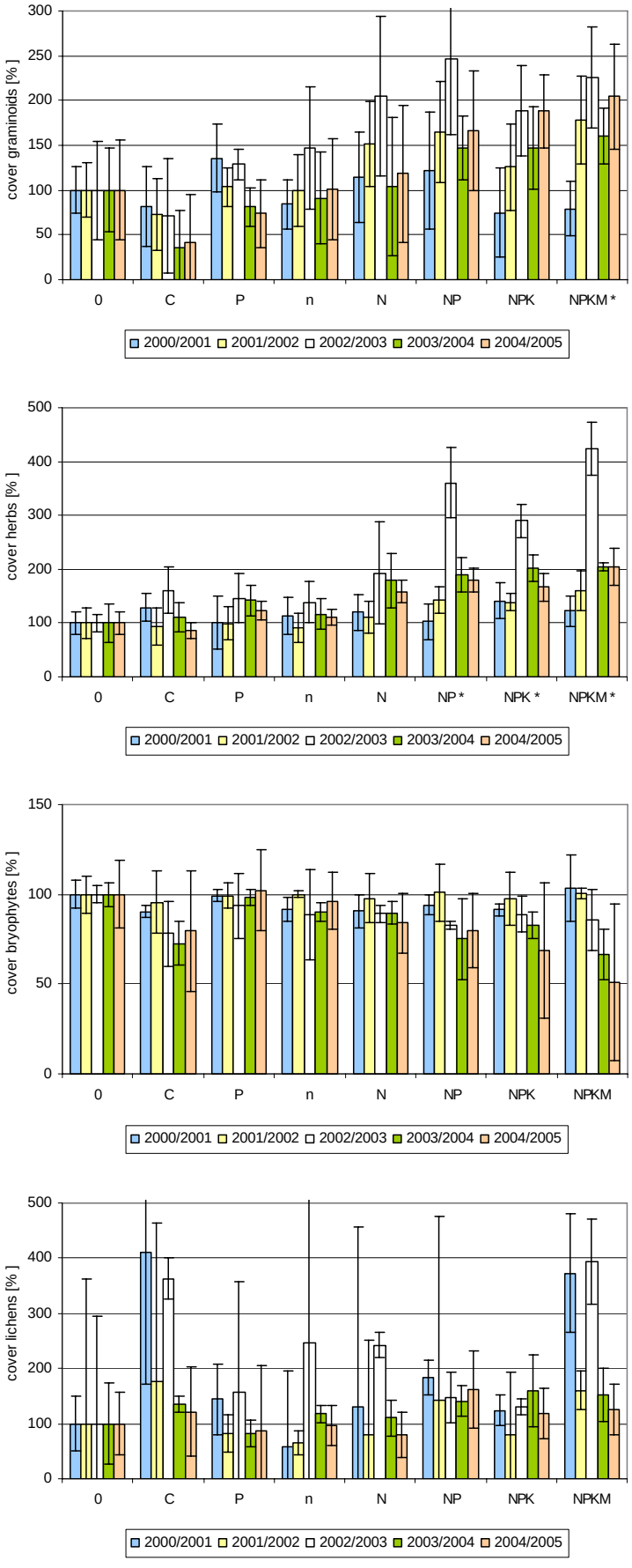

Figure 3.3. Cover of different vegetation layers. Treatment effects that are significantly different from the control for effect years (2001-2004) are marked with an "*****" at the inscription of the x-axis. Error: Mean absolute deviation from the mean.
The cover of the control is set at 100 % for each year. The following values are counted as 100 %: a) graminoids. 00/01: 22 %; 01/02: 24 %; 02/03: 10 %; 03/04: 25 %; 04/05: 21 %. b) herbs. 00/01: 23 %; 01/02: 27 %; 02/03: 9 %; 03/04: 26 %; 04/05: 45 %. c) bryophytes. 00/01: 110 %; 01/02: 102 %; 02/03: 105 %; 03/04: 96 %; 04/05: 74 %. d) lichens: 00/01: 3 %; 01/02: 8 %; 02/03: 4 %; 03/04: 17 %; 04/05: 23 %.

Figure 3.4 demonstrates the analysis of individual species. Only for *Bromus tectorum* and *Medicago minima* are significant effects detectable. For *Bromus tectorum* the term "treatment*year" is not significant but the treatment effect shows a 7-fold increase of the cover of *Bromus tectorum* for the NPK-treatment. In the case of the endangered species *Medicago minima* the treatment effect depends on the year; it was only in 2003/2004 that there was a significant increase, almost 4-fold, of *M. minima*-cover following the phosphorus treatment.

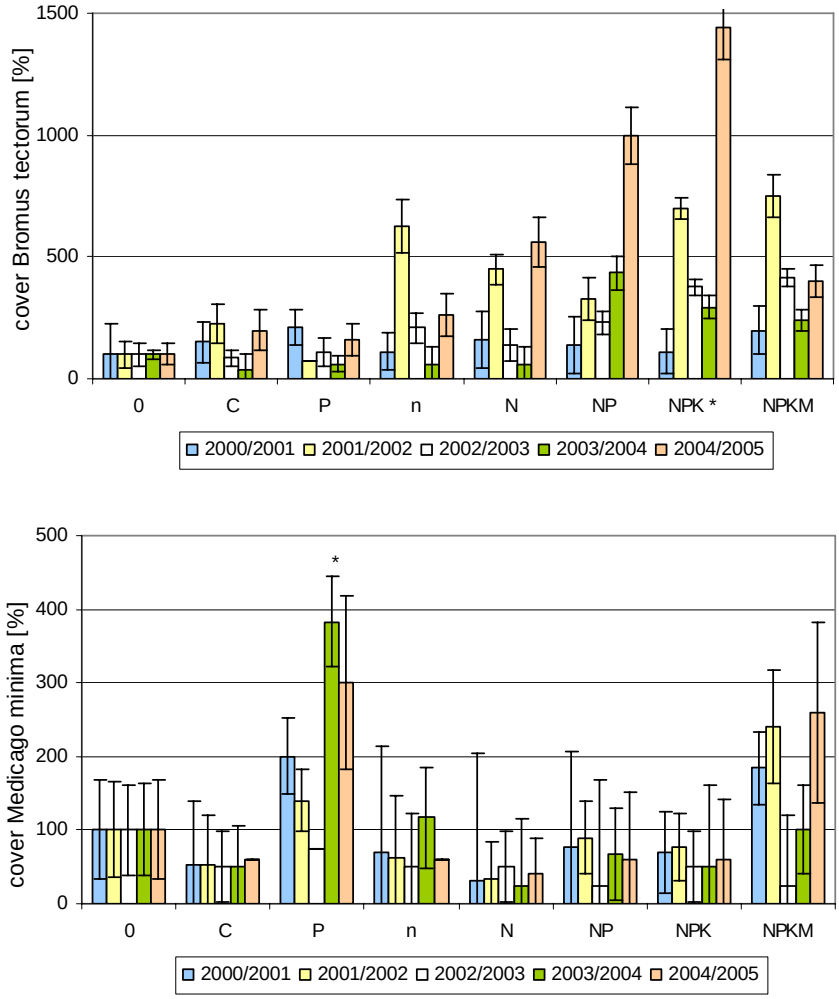

Figure 3.4. Cover of *Bromus tectorum* and *Medicago minima*. Treatment effects that are significantly different from the control for effect years (2001-2004) are marked with an "*****" at the inscription of the x-axis. Effects that are significant for a certain year are marked with an "*****" over the bar of the concerned year. Error: Mean absolute deviation from the mean.
The cover of the control is set at 100 % for each year. The following values are counted as 100 %: a) *Bromus tectorum*. 00/01: 0.8 %; 01/02: 0.4 %; 02/03: 1.3 %; 03/04: 1.8 %; 04/05: 0.5 %. b) *Medicago minima*. 00/01: 1.3 %; 01/02: 3 %; 02/03: 0.4 %; 03/04: 1.2 %; 04/05: 0.5 %.

Species composition and phytodiversity

Plant species composition and the temporal development of the plots were analysed by means of detrended correspondence analysis, as depicted in Figure 3.5. There is a strong correlation of bryophytes with the first axis: the cover of *Hypnum cupressiforme* decreases (r = -0.78) while the cover of *Tortula ruraliformis* increases (r = 0.90) with increasing values of the first axis. The investigated blocks are vaguely divided into a group where *Hypnum* is dominant (blocks X, Y, Z), located at the left side of the diagram, and a group with dominance of

Tortula (blocks V, W) located at higher values of the first axis. No separation between the different treatments can be observed. The second axis strongly reflects the investigated years: the relevés of the status quo year as well as that of the first effect year are located at low values of the second axis while the latest relevés are located at highest values of the second axis.

Phytodiversity is set between 15 and 42 species per 4-m² plot and is thus extraordinarily high. We tested total plant species richness as well as plant species richness of different plant functional types, life forms or phyto-sociological groups but no significant treatment effects were observed.

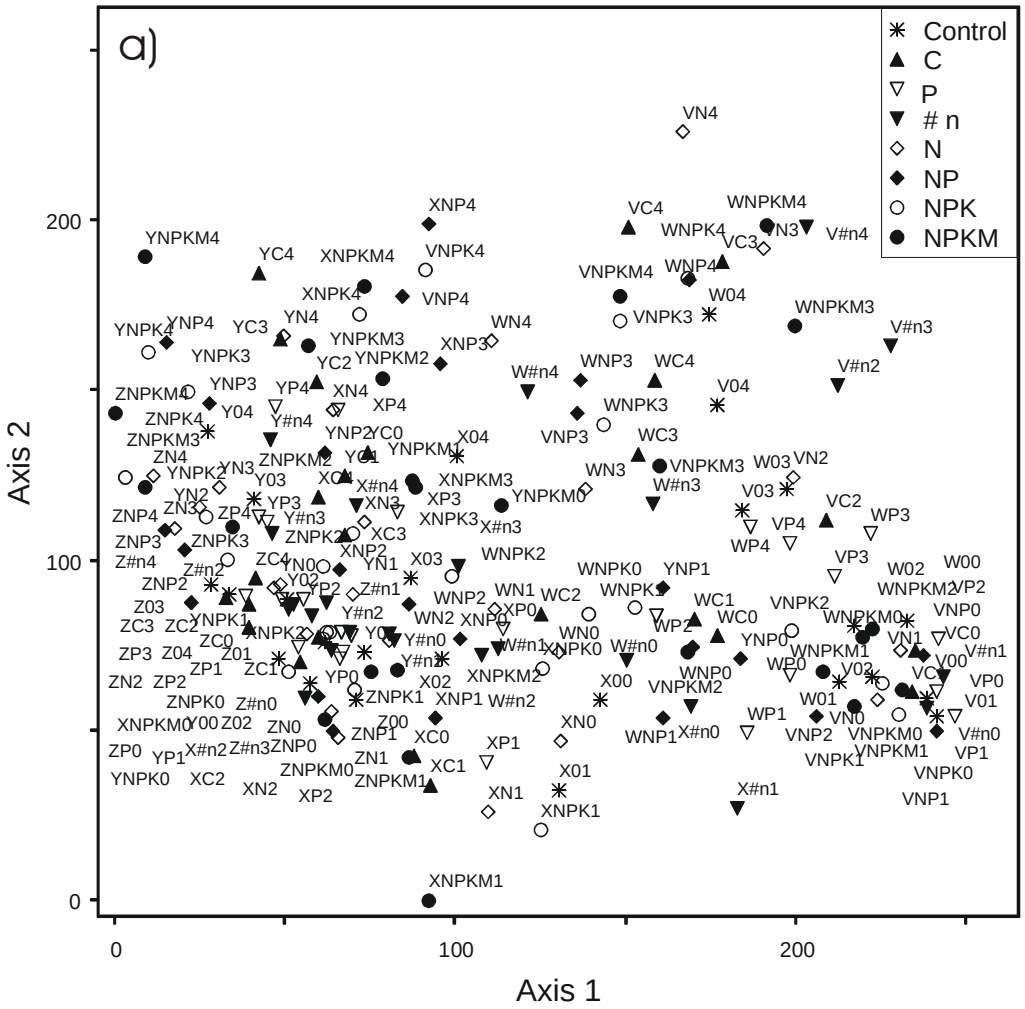

Figure 3.5a. DCA of the investigated plots for 5 years. Eigenvalues and lengths of gradient: First axis. 0.44; 2.5. Second axis: 0.21; 2.3. V, W, X, Y, Z: investigated block. 0, C, P, #n (= n), N, NP, NPK, NPKM: treatment plot. The number behind the plot name refers to the investigated year: 0: status quo relevés of 2000/2001. 1: relevés of 2001/2002. 2: relevés of 2002/2003. 3: relevés of 2003/2004. 4: relevés of 2004/2005.

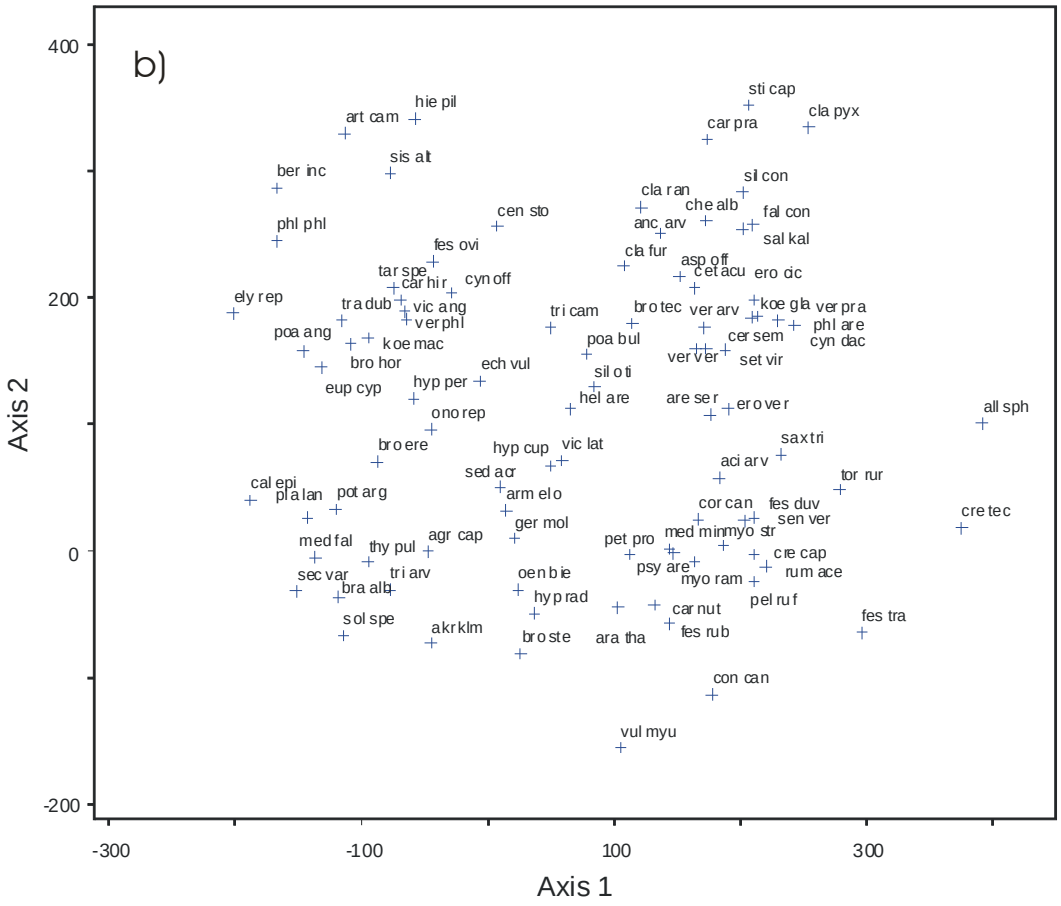

Figure 3.5b. species. agr cap: *Agrostis capillaris*, bro ere: *Bromus erectus*, bro hor: *Bromus hordeaceus*, bro ste: *Bromus sterilis*, bro tec: *Bromus tectorum*, cal epi: *Calamagrostis epigejos*, car hir: *Carex hirta*, cor can: *Corynephorus canescens*, cyn dac: *Cynodon dactylon*, ely rep: *Elymus repens*, fes ovi: *Festuca ovina* agg., fes duv: *Festuca duvalii*, fes rub: *Festuca rubra*, fes tra: *Festuca trachyphylla*, koe gla: *Koeleria glauca*, koe mac: *Koeleria macrantha*, phl are: *Phleum arenarium*, phl phl: *Phleum phleoides*, poa ang: *Poa angustifolia*, poa bul: *Poa bulbosa*, set vir: *Setaria viridis*, sti cap: *Stipa capillata*, vul myu: *Vulpia myuros*, aci arv: *Acinos arvensis*, all sph: *Allium sphaerocephalon*, anc arv: *Anchusa arvensis*, ara tha: *Arabidopsis thaliana*, are ser: *Arenaria serpyllifolia* agg., arm elo: *Armeria maritima* ssp. *elongata*, art cam: *Artemisia campestris*, asp off: *Asparagus officinalis*, ber inc: *Berteroa incana*, car nut: *Carduus nutans*, cen sto: *Centaurea stoebe*, cer sem: *Cerastium semidecandrum*, che alb: *Chenopodium album* agg., con can: *Conyza canadensis*, cre cap: *Crepis capillaris*, cre tec: *Crepis tectorum*, cyn off: *Cynoglossum officinale*, ech vul: *Echium vulgare*, ero cic: *Erodium cicutarium* agg., ero ver: *Erophila verna*, eup cyp: *Euphorbia cyparissias*, fal con: *Fallopia convolvulus*, ger mol: *Geranium molle*, hel are: *Helichrysum arenarium*, hie pil: *Hieracium pilosella*, hyp per: *Hypericum perforatum*, hyp rad: *Hypochaeris radicata*, med fal: *Medicago falcata*, med min: *Medicago minima*, myo ram: *Myosotis ramosissima*, myo str: *Myosotis stricta*, oen bie: *Oenothera biennis* s.l., ono rep: *Ononis repens*, pet pro: *Petrorhagia prolifera*, pot arg: *Potentilla argentea* agg., psy are: *Psyllium arenarium*, pla lan: *Plantago lanceolata*, rum ace: *Rumex acetosella*, sal kal: *Salsola kali* ssp. *tragus*, sax tri: *Saxifraga tridactylites*, sec var: *Securigera varia*, sed acr: *Sedum acre*, sen ver: *Senecio vernalis*, sil con: *Silene conica*, sil oti: *Silene otites*, sis alt: *Sisymbrium altissimum*, sol spe: *Solidago* spec., tar spe: *Taraxacum* spec., thy pul: *Thymus pulegioides*, tra dub: *Tragopogon dubius*, tri arv: *Trifolium arvense*, tri cam: *Trifolium campestre*, ver spe: *Verbascum* spec., ver arv: *Veronica arvensis*, ver pra: *Veronica praecox*, ver ver: *Veronica verna*, vic ang: *Vicia angustifolia*, vic lat: *Vicia lathyroides*, akr klm: Acrocarpi indet., bra alb: *Brachythecium albicans*, hyp cup: *Hypnum cupressiforme*, tor rur: *Tortula ruraliformis*, cet acu: *Cetraria aculeata*, cla fur: *Cladonia furcata*, cla pyx: *Cladonia pyxidata*, cla ran: *Cladonia rangiformis*, pel ruf: *Peltigera rufescens.*

Species height

The results of the measurement of the height of individual species are shown in Figure 3.6. *Bromus tectorum, Erodium cicutarium* agg. (leave and stem), *Medicago minima, Psyllium arenarium, Salsola kali* ssp. *tragus* and *Silene conica* are significantly higher in the case of a strong nutrient input (NP, NPK or NPKM-treatment). The opposite effect can be seen in the case of *Corynephorus canescens*, which is significantly smaller following NPKM addition.

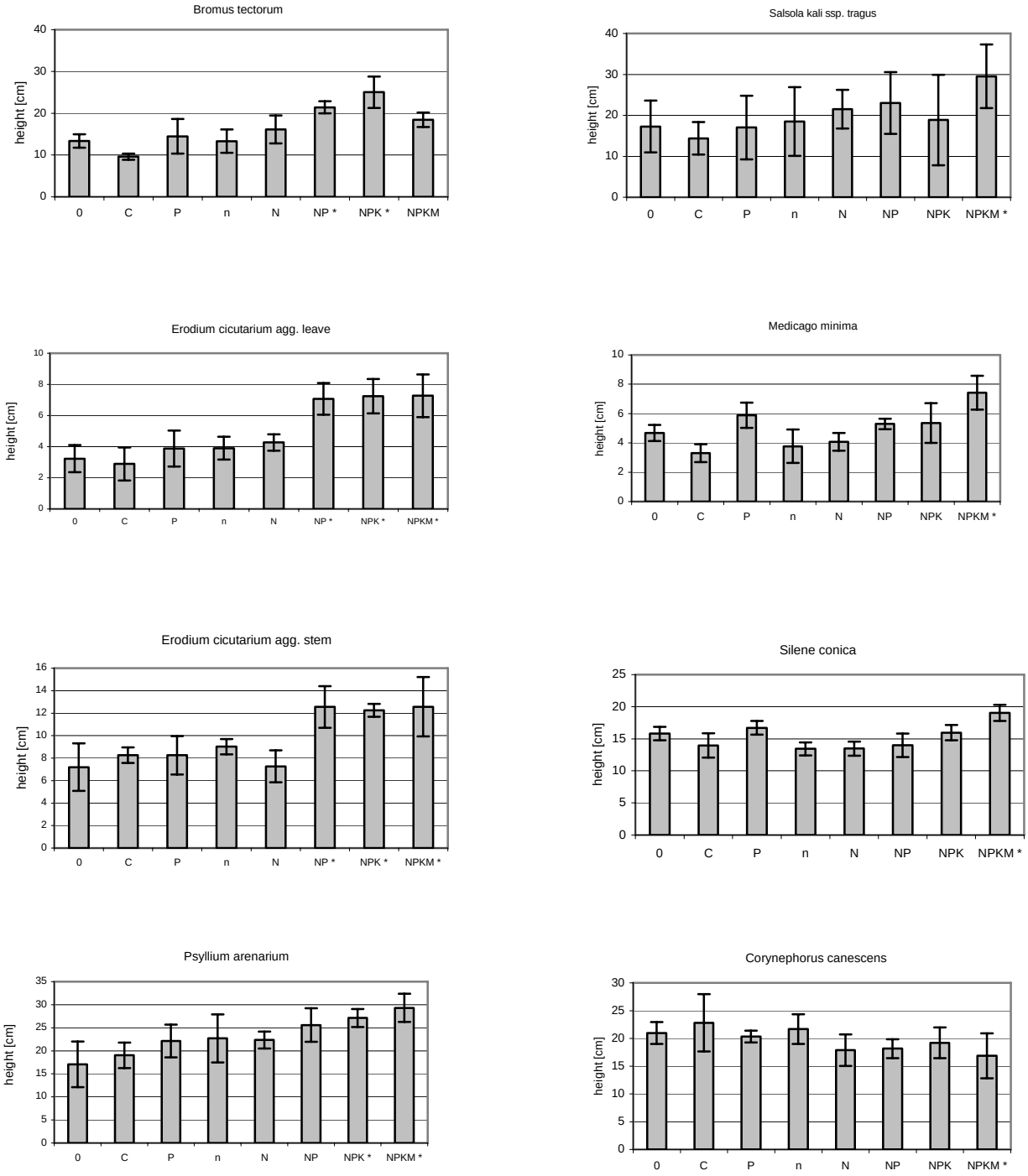

Figure 3.6. Height of certain species in the year 2004. Treatments that are significantly different from the control are marked with an "*****" at the inscription of the x-axis. Error: Mean absolute deviation from the mean.

The height of the species *Arenaria serpyllifolia* agg., *Carex hirta*, *Centaurea stoebe*, *Cynodon dactylon*, *Euphorbia cyparissias*, *Helichrysum arenarium*, *Phleum arenarium*, *Saxifraga tridactylites*, *Sedum acre*, *Senecio vernalis* and *Setaria viridis* is increased by the NP, NPK and NPKM treatments, but statistical analyses revealed that the significance level of 5 % was exceeded, usually due to small sample sizes.

Seed production

An influence of the nutrient treatment on the individual plant is also reflected in the case of the number of seeds per individual. For *Bromus tectorum*, the seed production is about thrice as high with NP, NPK or NPKM-addition (Figure 3.7) while for *Erodium cicutarium* agg. the number of infructescences per individual is 9-fold higher with the NPK-treatment than with the control. The high seed production of *Centaurea stoebe* is even doubled in the case of N-addition. For the species *Euphorbia cyparissias*, *Sedum acre* and *Silene conica* no significant effects are observed.

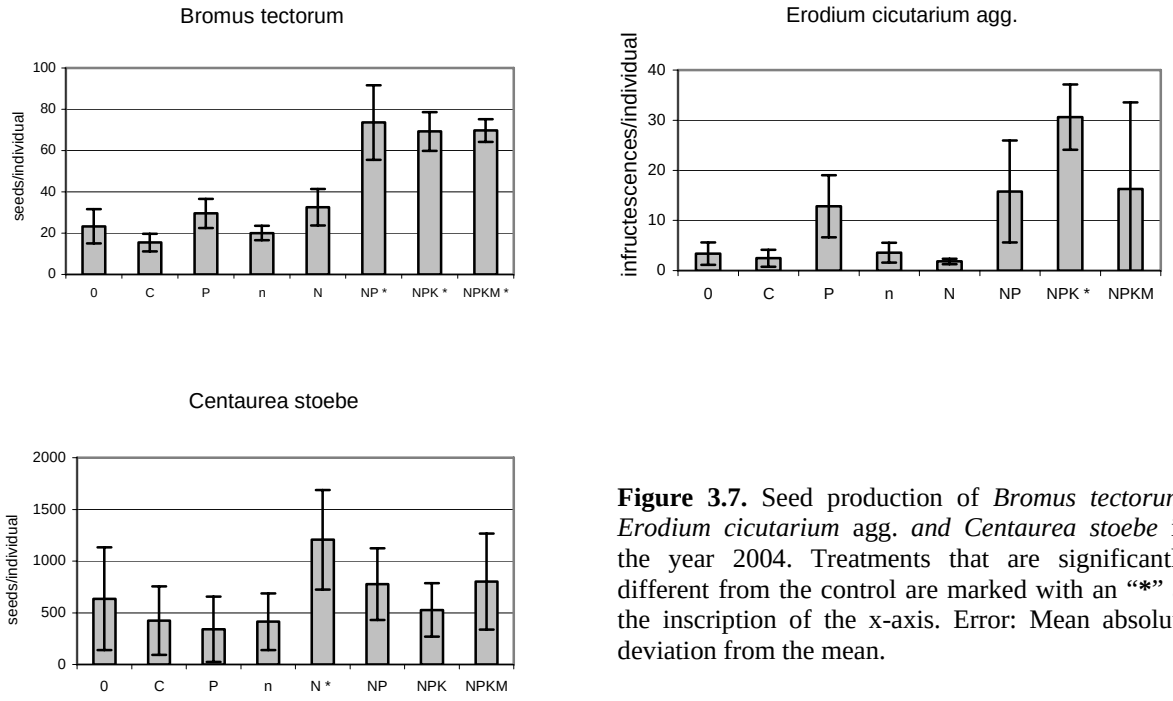

Figure 3.7. Seed production of *Bromus tectorum*, *Erodium cicutarium* agg. *and Centaurea stoebe* in the year 2004. Treatments that are significantly different from the control are marked with an **"*"** at the inscription of the x-axis. Error: Mean absolute deviation from the mean.

Discussion

Influence of the year

In this experiment throughout all investigated variables, the influence of the year is very often the most significant factor. This is due to two reasons. First, it is possible that the effects of the nutrient addition will be enhanced in successive years and that the enrichment of nutrients must exceed a certain threshold before an effect is detectable. This is analysed by the interaction "treatment*year".

Second, some effects are dependent on the year but not on the treatment (significant main effect "year"). Since the 5 observed years are very different concerning the weather conditions, it is very likely that the weather, probably the precipitation, has strong impact on the vegetation. This is confirmed by the low cover of the vegetation layers and the lower above-ground phytomass production in the dry year 2003. The strong influence of the year on all variables is an indication that water is a limiting factor controlling the ecosystem. Other studies have also pointed out the influence of the precipitation rate on phytomass production for arid environments (Le Houérou et al.1988, Süss et al. submitted).

Treatment effects

For a synopsis of the results, all investigated variables with significant treatment effects are summarised in Table 3.7.

		C	P	n	N	NP	NPK	NPKM
soil	N_{min}	-	-	-	1.4	-	-	-
	P*	-	5.2	-	-	5.0	4.4	4.4
	K	-	-	-	-	-	2.0	1.8
	pH	-	-	-	-	-	-	-
phytomass	graminoids + herbs	-	-	-	1.9	2.4	1.8	2.4
	roots	-	-	-	-	-	-	-
	cryptogams	-	-	-	-	-	-	-
	litter	-	-	-	-	-	-	-
cover	graminoids	-	-	-	-	-	-	1.9
	herbs	-	-	-	-	2.2	2.0	2.5
	bryophytes	-	-	-	-	-	-	-
	lichens	-	-	-	-	-	-	-
	Bromus tectorum	-	-	-	-	-	7.0	-
	Medicago minima**	-	3.8	-	-	-	-	-
species height	Bromus tectorum	-	-	-	-	1.6	1.8	-
	Erodium cicutarium agg. leave	-	-	-	-	2.2	2.2	2.3
	Erodium cicutarium agg. stem	-	-	-	-	1.7	1.7	1.7
	Psyllium arenarium	-	-	-	-	-	1.6	1.7
	Salsola kali ssp. tragus	-	-	-	-	-	-	1.7
	Medicago minima	-	-	-	-	-	-	1.6
	Silene conica	-	-	-	-	-	-	1.2
	Corynephorus canescens	-	-	-	-	-	-	0.8
seed production	Bromus tectorum	-	-	-	-	3.2	3.0	3.0
	Erodium cicutarium agg.	-	-	-	-	-	9.1	-
	Centaurea stoebe	-	-	-	1.9	-	-	-

Table 3.7. Summary of the significant effects. For each significant treatment the factor of its increase/decrease in relation to the control is given. *: Factor for the year 2004. **: Factor for the relevé 2003/2004. "-": No significant effect detectable.

Effects on the soil

The results of the soil analyses demonstrate that in the beginning of the experiment, nitrogen as well as phosphorus and potassium contents were homogeneous over the experimental plots and low, which is typical for sand dunes.

Regarding mineral nitrogen, only in one case (N-treatment) the nutrient content of the soil is significantly higher than in the control. According to Boorman & Fuller (1982) and ten Harkel et al. (1998), storage in the biomass is likely. As the nutrients are applied 10 times a year rather than once in high dosages, leaching losses owing to rainfall are likely to be small. Therefore we assume that nitrogen was taken up by the plants or immobilised. Hence either an increase of phytomass or an increase of plant nitrogen content can be expected, and the non-accumulation of mineral nitrogen in the soil can be interpreted as a hint of a nitrogen-limitation in the ecosystem. This is different for phosphorus and potassium, both of which are accumulated after treatment with these elements. Boorman & Fuller (1982) reported the same results following nitrogen, phosphorus and potassium fertilisation of coastal dunes.

Effects on the vegetation

As the phytomass analyses as well as the analyses of the different vegetation layers have shown, above-ground phytomass of graminoids, herbs and cryptogams is much more affected by the nutrient treatments than below-ground phytomass, which does not increase significantly with increasing nutrient supply. Other studies have also pointed out that fertilisation has only weak effects on root phytomass (Morecroft et al. 1994, Day 1996) or even causes it to decrease (Bardgett et al. 1999). Above-ground phytomass production of phanerogams (graminoids + herbs) was doubled by N, NP, NPK and NPKM treatments, giving a clear indication of nutrient limitation. The effect was not pronounced, however. The above-ground productivity of the control plots, varying from 55 to 131 g * m^{-2}, falls distinctly short of the range for temperate grasslands of 200-1500 g * m^{-2} (Whittaker 1970). Even after 4 years of treatment with all macro- and micronutrients, productivity remained on a low level. Three reasons could have contributed to this weak response:

1) Water as a limiting factor. Snyman (2002) also reported greater responses to nutrient additions in regions with high rainfall, because there is insufficient soil water in arid ecosystems, and Mamolos et al. (2005) stated that the nutrient limitation of herbaceous grasslands depends on the water supply.

2) Inherently low growth potential of the plants adapted to nutrient-poor soils. As Chapin III et al. (1986) pointed out, “plant communities occupying infertile sites are not always the most responsive to nutrient addition”.
3) In nutrient-poor soils added nutrients are often immobilised by microbial uptake. At our study site, phytomass samples have been taken and will be analysed. The results will show to what extent the nutrients were taken up by the vegetation.

The analyses of both phytomass and cover of different vegetation layers also demonstrate that the low-dosage nitrogen treatment (25 kg * ha^{-1}* a^{-1}) does not have any considerable effect on the vegetation, whereas nitrogen in high dosage (100 kg ha^{-1}* a^{-1}) in some cases influences the investigated variables. This can be interpreted as an indication that the atmospheric deposition of nitrogen in our ecosystem has no significant influence on vegetation parameters of early successional stages.
In most cases nitrogen even in high dosages is only effective in combination with other nutrients such as were applied in the NP, NPK or NPKM treatment. Mostly, the NPKM treatment has the strongest effect. This demonstrates that nitrogen is not the only limiting factor and in case of an improved nitrogen supply other macro- and micronutrients become limiting. A co-limitation of nitrogen and phosphorus, or an enhanced effect in case of a combined fertilisation by both, has often been reported, especially in the case of calcareous grasslands (Bobbink 1991, Davy & Bishop 1984, Esselink & van Gils 1994, Kooijman et al. 1998, Morecroft et al. 1994) and dry grasslands (Mamolos et al. 2005).
Regarding the organic carbon treatment, only a tendency towards an increase in cryptogam phytomass is observed. It remains to be seen whether that effect will become significant after some more years of carbon treatment. Together with the lack of significant increase with high nutrient addition but, on the contrary, a tendency for their phytomass to decrease in the case of the NPKM treatment, this demonstrates that in contrast to the phanerogams, cryptogams are not limited by nutrients but probably are good stress-tolerators especially in the case of nutrient-poor conditions. Ingerpuu et al. (1998) and Thormann & Bayley (1997) reported an increase in bryophyte cover after fertilisation. A negative response of bryophyte species richness to fertilisation is discussed by Aude & Ejrnaes (2005).

The fact that until now no significant effects on plant species richness or on plant species composition have been observed is probably due to the ecosystem in which the investigation took place. The site-specific plant species of early successional stages of sand ecosystems are

good stress-tolerators according to the CSR-model of Grime (1979), and competition for light is not important due to a gappy cover of phanerogams. In other nutrient-addition experiments, an increase of phytomass leads to competition for light and thus often therophyte species are outcompeted by perennials, often grasses (Boorman & Fuller 1982, Davy & Bishop 1984, Mamolos et al. 1995). In our pioneer stages, addition of large amounts of nutrients increased not only the cover of graminoids but also that of herbs, to an even greater extent. Therophytes are still present after 4 years of NPKM-treatment and a higher phytomass on these plots is mainly due to a higher phytomass of species, such as *Centaurea stoebe*, which develop late in the vegetation period. Therefore therophytes that are dependent on light in the early spring are not yet shaded out. So presumably due to a well-balanced niche-partitioning, species composition is not affected within a few years by nutrient addition in that kind of ecosystem, with these pioneer plant communities. But as Süss et al. (2004a) have already pointed out for mid-successional stages, after a longer period we would expect grass-encroachment and an accumulation of litter in case of the highly nutrient-supplied plots, which causes a decrease of plant species richness.

Regarding individual species, *Bromus tectorum* is significantly promoted by NP, NPK or NPKM-addition in its cover, height and seed production. Auman et al. (1998) also found an increased plant height and fecundity for *Bromus tectorum* near dung sites. This is a grass species of earlier successional stages with a ruderal tendency. Together with the promotion of the ruderal plant species *Psyllium arenarium* and *Salsola kali* ssp. *tragus* in the case of N, NP, NPK or NPKM treatments, these results can be interpreted as predicting a ruderalisation tendency at these plots in future. The fact that the Fabaceae species *Medicago minima* is supported by phosphorus addition is in accordance with previous investigations in other ecosystem-types (Bobbink 1991, Mamolos et al. 1995).

The decrease in height of *Corynephorus canescens* with NPKM-addition is consistent with earlier studies which report a synecological preference of nutrient-poor sites (Marshall 1967).

Besides the above-mentioned significant increases of the height of 6 species, we found a tendency towards height increase for another 11 species. This shows that nearly all of the 19 studied species benefit from nutrient addition.

In total, our results lead to the conclusion that in the case of these pioneer stages, mainly the individuals are influenced by the different treatments and after four years of treatment, the community is not affected. Apparently after 4 years of treatment, competition is not strong enough for species to outcompete one another. But since species with a ruderal tendency are

especially strongly influenced, this can already be interpreted as an indicator of the expected ruderalisation in mid-successional stages.

Conclusions for the management of grazed ecosystems

In the case of sheep grazing, Bergmann (2004) determined a mean nutrient input of 2.4-5.2 kg N ha^{-1}* a^{-1} and 0.55-1.51 kg P ha^{-1}* a^{-1} resulting from dung deposits and 3.7-7.7 kg N ha^{-1}* a^{-1} and 0.003-0.007 kg P ha^{-1}* a^{-1} resulting from urine spots for the same ecosystem interpolated over the whole paddock. If the dung pellets are accumulated at small spots, nutrient input at these distinct spots is 289-382 kg N ha^{-1}* a^{-1} and 71-89 kg P ha^{-1}* a^{-1} for sheep. In case of donkeys - which are also used for the management of dry sandy ecosystems (Lamoot et al. 2005, Zehm et al. 2004) - a mean nitrogen input of 223 kg N ha^{-1}* a^{-1} at faeces accumulation sites was measured (Süss et al. in prep.). At urine spots, also potassium has a remarkable influence (Brenner et al. 2004). The values of the accumulated dung depositions fit well with our N, NP, NPK or NPKM-treated plots. Total nitrogen content is higher at the animals' excreta spots but this nutrient input is applied only once, whereas in the present experiment we added mineral nitrogen over a period of several years; hence mineral nitrogen input and the effects on the vegetation can be compared. So we can conclude that in the case of an accumulation of faeces (which often occurs in the case of equids' grazing) a very concentrated nutrient input can lead to an increase of phytomass and a ruderalisation tendency which can be more distinct in mid-successional stages than early pioneer stages. Together with the fact that the animals often refuse to graze at these sites, a patchy distribution of nutrients can develop which will lead to small-scale ruderalised sites.

If the faeces pellets are spread homogeneously over the whole paddock, which is often the case with sheep grazing in our system - due to the grazing regime with high stocking rates at small paddocks for a very short period - the influence on the vegetation is expected to be negligible because of the very low nutrient inputs as determined by Bergmann (2004). Additionally, it has to be considered that the nutrient input of the faeces and urine patches is derived from the phytomass on which the animals have been grazing; hence only a horizontal nutrient transfer can be expected, which is only detectable in the case of an accumulation of faeces. Thus it is important that an adequate grazing regime is chosen carefully, especially that those grazing regimes where faeces-accumulation sites can occur are not repeated over several years (Süss et al. submitted).

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Chapter 4:
The interrelationship between productivity, plant species richness and livestock diet: a question of scale?

Abstract

Question: What relationship exists between productivity, plant species richness and livestock diet? Are the results dependent on scale?

Location: A sheep-grazed Koelerio-Corynephoretea sandy habitat of the Northern Upper Rhine (Germany) as a low-productivity model system.

Methods: The investigation was carried out for three years at fine-grain scale (2 m²) and for two years at broad scale (79 m²). Productivity was measured by means of weighed aboveground phytomass for fine-grain scale and colour-infrared (CIR) aerial orthophotos of the same system for fine-grain and broad scale. For both scales, total numbers of vascular plant species and numbers of endangered vascular plant species were extracted from current vegetation relevés. Additionally, we obtained data on livestock diet (grazed phytomass, crude protein content).

Results: Statistical analyses show an influence of the year on all variables; relationships between variables are not significant in every year. Species richness and number of endangered species are negatively related to productivity at fine-grain scale while crude protein content and grazed phytomass are positively related to productivity. At broad scale the diversity-productivity relationship shows a “hump” with highest species numbers in middle pioneer stages; numbers of endangered species are highest in all pioneer stages.

Conclusions: We found a strong impact of scale and year on the diversity-productivity relationship. It is inappropriate to analyse only small plots (2 m²), and it is necessary to study different years. This vegetation complex is dependent on grazing impact; thus there is an inversely proportional relationship between nature conservation value (high diversity) and livestock nutrition.

Abbreviations: CIR: colour-infrared, K: Koelerion glaucae, F: *Festuca duvalii/ trachyphylla*-community, A: Armerio-Festucetum trachyphyllae

Introduction

The relationship between plant species richness and productivity (phytomass production) is a subject of substantial interest in vegetation ecology. Most often proposed is the model of a unimodal hump-shaped relationship with a diversity maximum at medium productivity levels, as proposed, e.g., by Grime (1973) and Al Mufti et al. (1977). For a great variety of ecosystems this relationship has been described by many authors (e.g. Abramsky & Rosenzweig 1984, García et al. 1993, Huston & DeAngelis 1994). However, concerning grassland communities, some authors also described positive relationships (e.g. Pfisterer et al. 2004) or negative ones (Goldberg & Miller 1990, Gough et al. 2000) but often the investigations were based on "experimental communities" and fertilisation experiments. As Waide et al. (1999) and Fridley (2002) have already proposed, negative relationships most often occur in the case of "experimental plant communities" (e.g. Tilman et al. 1996, Gough & Grace 1998, Gough et al. 2000), where higher rates of fertilisation generally reduce diversity (Rajaniemi 2003). As was recently described by Lepš (2004), doubts have been expressed especially by vegetation ecologists as to whether "experimental plant communities" reflect general relationships of diversity rules "in the real world"; these doubts were contradicted by Schmid & Hector (2004) but recently supported by Kahmen et al. (2005).

In our investigation, we focus on sheep-grazed Koelerio-Corynephoretea communities. These plant communities are characterised by dryness and poverty of nutrients, and thus have low productivity values. Within these open habitats there is a productivity gradient from pioneer communities (Koelerion glaucae) to denser grassland (Armerio-Festucetum trachyphyllae). These habitats are of high conservation value because many threatened plant communities (e.g. Jurineo-Koelerietum glaucae, Armerio-Festucetum trachyphyllae) and endangered plant species (*Koeleria glauca, Jurinea cyanoides, Armeria maritima* ssp. *elongata*) are typical. Numerous studies have shown that sheep grazing is an ideal method for the management of various low-productivity ecosystems (Kooijman & van der Meulen 1996, Hellström et al. 2003) but for the studied plant communities few data are available (Schwabe & Kratochwil 2004, Süss et al. in prep). In the case of spontaneous succession, a progressive ruderal grass-encroachment with a decrease of plant species richness is observed (Süss et al. 2004).

Therefore the relationship between diversity and productivity is closely related to economic aspects, as discussed, e.g., by Tilman (1999) and Beierkuhnlein & Jentsch (2005), and it is important to know whether the agroeconomical importance for livestock nutrition correlates with goals of nature conservation.

An intensive discussion about the importance of scale for the kind of relationship between productivity and plant species richness has recently developed (e.g. Oksanen 1996, Mittelbach et al. 2001, Allock & Hik 2003, Chalcraft et al. 2004). According to Oksanen (1996), the hump-shaped curve might often be an artefact due to plot size, but Roscher et al. (2005) found identical positive species richness as well as aboveground productivity relationships on large (20 x 20 m) and on small (3.5 x 3.5 m) plots. In case of sand ecosystems we also found it very important to investigate at both fine-grain and broad scales, because on the one hand species richness is already high at small-sized plots while on the other hand various vegetational subtypes exist at a broader scale.

For broad-scale investigation of the relationship between diversity and productivity, it is important to avoid employing destructive productivity measurements on experimental plots. Therefore remote sensing can be an ideal tool for investigating productivity at a broad scale. As Turner et al. (2003) stated, there is consensus about the need for more data linking patterns of primary productivity and large-area estimates of species-richness and abundance. Cousins & Ihse (1998) found an interpretation accuracy of 95-99 % while using CIR-photos for biotope mapping. Therefore we used on one hand the aboveground peak standing crop as the most common estimate for net primary productivity in grasslands (Scurlock et al. 2002). On the other hand we developed a procedure of imaging analysis by using CIR (colour-infrared) aerial photos (7.5 cm $pixel^{-1}$) to measure the spectral reflectance factors of vegetation and find their relationship to productivity characteristics. By using both methods we were able to validate the CIR approach and thus to investigate the relationship between plant species richness and productivity at a broader scale in order to examine whether the relationship is scale-dependent.

We studied different years, because we hypothesised that this is important for analysing general rules, as productivity is also strongly dependent on abiotic parameters such as annual precipitation (e.g. Abramsky & Rosenzweig 1984, Pignatti & Pignatti 1999, Schwabe & Kratochwil 2004). Although the literature includes many studies dealing with the relationship between diversity and productivity, there are hardly any investigations covering different years in the same investigation area (exception, e.g., Hiremath & Ewel 2001).

To highlight general rules governing productivity, plant species richness and livestock nutrition in a threatened low-productivity ecosystem we focus on the following questions:

1) What relationship can be worked out between aboveground phytomass and plant species richness as well as between aboveground phytomass and the number of endangered plant species a) with the peak standing crop method? b) with the CIR analysis method?
2) What relationship exists between plant species richness and its agroeconomical importance for livestock nutrition?
3) Can we detect different kinds of relationships at different scales?
4) What conclusions can be drawn for the management of threatened habitats (in our case, Koelerio-Corynephoretea communities) by combining questions 1) and 2)?

Materials and methods

Study area

The investigation took place during 3 vegetation periods (2000–2002) in the Northern Upper Rhine Valley (Germany) about 30 km south of Frankfurt/Main (Hesse), near Darmstadt. A nature reserve and Flora-Fauna-Habitat area ("Ehemaliger August-Euler-Flugplatz von Darmstadt"), a former 71-ha airfield, was used as a model area for inland sand ecosystems. The substrate is sand which had been blown-out from calcareous Rhine deposits during late glacial and post-glacial periods. From the eastern part to the western part of the investigation area the primarily calcareous topsoil horizon is becoming progressively acidified, to a slight degree, by successional processes. The pH ranges from 5.9 to 7.5 in the topsoil (Bergmann 2004). Mean annual temperature is about 9 °C. These features, in combination with the rather low mean annual precipitation rate of about 700 mm $year^{-1}$ (Walther & Lieth 1967), characterise the dry and warm climate of the region. In relation to the long-term average climatic conditions the three investigated years can be classified as "normal" years (2000: mean temperature 11.6 °C, sum of precipitation 759 mm, 2001: 10.8 °C, 753 mm, 2002: 11.2 °C, 778 mm, data from Frankfurt/Main airport, Internet) although there were higher precipitation rates in the first months of 2001 than in the other years (sum of precipitation January to April 2000: 175 mm, 2001: 303 mm, 2002: 214 mm). These months have a strong impact on the yearly vegetation development because grazing already starts in May.

The vegetation of the investigation area is characterised by plant communities belonging to early successional stages of Koelerion glaucae in the eastern part and more consolidated stages with slight topsoil acidification such as the Armerio-Festucetum trachyphyllae in the western part of the area.

In 1999, extensive sheep-grazing came into use as a management tool in order to protect a mosaic of early successional stages and to reduce monodominant grass species such as, e.g., *Cynodon dactylon* or *Elymus repens*. In the years 2000 and 2001, about 170 sheep grazed in paddocks of ca. 3-4 ha for 10-14 (sometimes 20) days. In 2002, the grazing regime was changed and about 400 sheep grazed in small paddocks, ca. 1 ha, for 1-9 days. The paddocks were grazed as long as an adequate food supply could be guaranteed. Grazing took place in the period from late spring to summer. It began in May in the Koelerion glaucae parts of the study site, which are the low-productivity areas where peak standing crop is reached in May. From June to early August, when the maximum amount of phytomass in the western vegetation communities of the Armerio-Festucetum trachyphyllae is reached, these parts of the investigation area were grazed.

Sampling design and plant species richness

For further analyses the vegetation was assigned according to the vegetational gradient. Therefore the three vegetation types "Koelerion glaucae (K)", "*Festuca duvalii/trachyphylla*-community (F)" and "Armerio-Festucetum trachyphyllae (A)" were distinguished.

For broad-scale investigation, throughout the whole area, a grid with a mesh width of 65 m was established (Zehm & Zimmermann 2004). Just before grazing began, vegetation relevés were taken with a radius of 5 m (79 m²) at every grid point. The vegetation was recorded according to the cover-abundance scale of Barkman et al. (1964). The relevés of the year 2001 are used for further analyses. Nomenclature follows Wisskirchen & Haeupler (1998).

For fine-grain analyses, in the same vegetation types 46 temporarily ungrazed plots, each 1 m x 2 m, were established by means of small metal baskets (mini-exclosures) within the annual grazing period (see Figure 4.1). The location of the baskets was determined by evaluating how best to represent the various vegetational subtypes of the vegetation type concerned. In the next year each basket was placed directly beside the site of the year before. Exactly adjacent to each basket, a complementary grazed plot was sampled as well. The vegetation of the mini-exclosures was also recorded according to the cover-abundance scale of Barkman et al. (1964) just before grazing began.

By using the vegetation data, vascular plant species richness was calculated for every broad-scale and every fine-grain plot. Like other authors, we only used the vascular plant species, because bryophytes and lichens were neither sampled for peak standing crop analyses nor do

they contribute to the red-intensity of the CIR-photos. Additionally, we analysed the number of endangered plant species (according to the Red Data Book of Korneck et al. [1996]). Throughout the investigation area, the endangered species *Allium sphaerocephalon, Armeria maritima* ssp. *elongata, Festuca duvalii, Helichrysum arenarium, Koeleria glauca, Medicago minima, Phleum arenarium, Silene conica, Silene otites* and *Stipa capillata* are present.

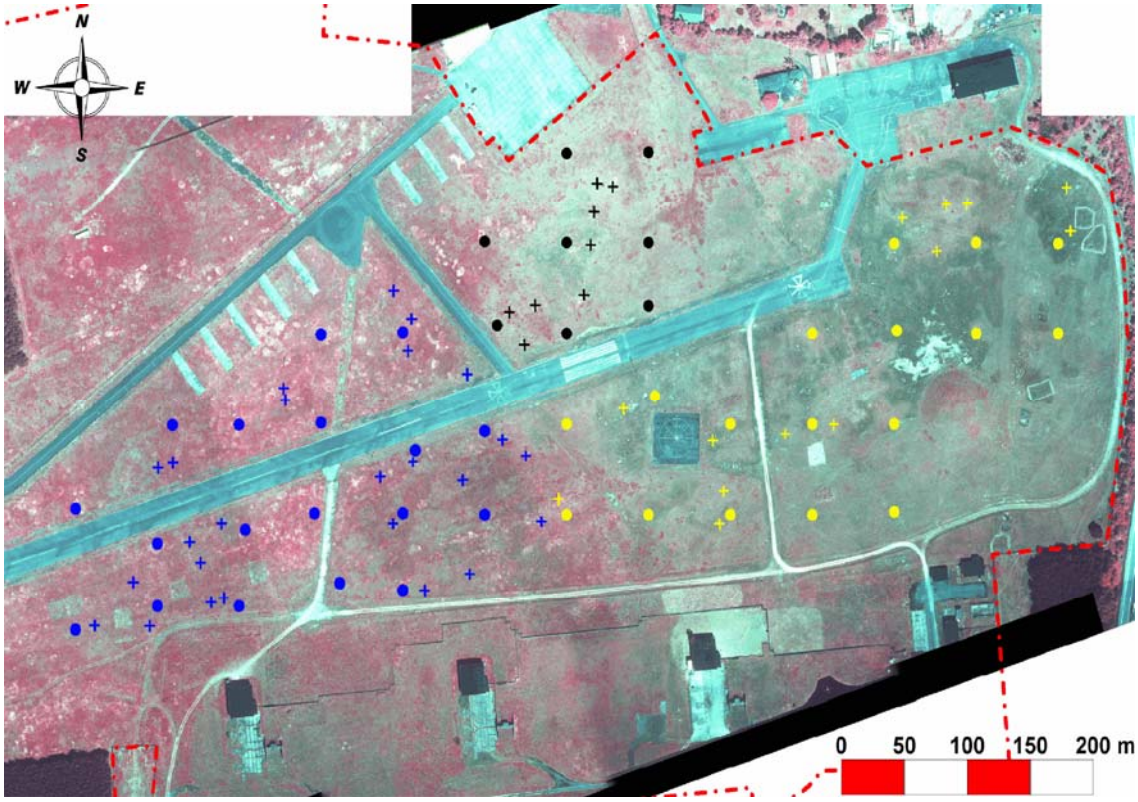

Figure 4.1: CIR aerial photo of the investigation area (2001). Areas with high productivity are deep red. Grid plots 5 m in radius are marked with filled circles, and the locations of the "mini-exclosures" are marked with crosses. The plots of the Koelerion glaucae are coloured yellow, those of the F-vegetation type black and those of the Armerio-Festucetum trachyphyllae blue.

Calculating productivity

a) by means of CIR aerial photos

In the years 2000 and 2001 in May (just before grazing began), CIR (colour-infrared) aerial photos of the whole investigation area were taken by means of a lens with a focal distance of 30 mm and a Kodak CIR film 2443 (flight altitude ca. 900 m; scale 1:2500). The vegetation of vascular plants shows a specific spectral reflectance in the range of the near infrared spectrum, hence sensors sensitive to radiation in the infrared part of the electromagnetic spectrum are used. Below-ground vegetation is not taken into account with this method.

Within a wavelength of 400-700 nm, pigments of the leaves are most important for the specific reflectance (Hildebrandt 1996). In the near infrared (700-1300 nm), the structure of the mesophyll causes the specific spectral reflectance and different types of plants can be

distinguished (e.g., Fabaceae species with intensely red colour). Schmieder et al. (2002) used a similar method to evaluate the vitality of reed belts according to red values of the CIR-photo. We used the grey-values of the red-channel (in the following named "red values") to analyse the different spectral reflectance characteristics of the plots. Due to the usage of 8 bit, $2^8 = 256$ grey-values can be displayed, thus the scale ranges from 0 to 255 and higher values represent areas of high chlorophyll activity. Plots at the broad scale as well as those at the fine-grain scale were analysed with this method.

b) by means of peak standing crop analyses

Immediately after the grazing period of each paddock the vegetation of the mini-exclosures was mown by electric clippers up to stubble-field-height, about 2 cm, dried for 48 h at 70 °C and afterwards weighed. The peak standing crop method is very commonly used for estimating productivity but net primary production is underestimated because simultaneous growth and death are not accounted for (Long et al. 1989). As with the CIR-approach, below-ground phytomass was also not taken into account. Nevertheless, this method is applied in many phytomass investigations (e.g. Bonser & Reader 1995, Allock & Hik 2003, Osem et al. 2004).

Livestock nutrition

The crude protein content of the livestock's diet is an important quality parameter for animal nutrition (Smallegange & Brunsting 2002) and was therefore chosen as a model parameter for this investigation. Crude protein content of the dried phytomass resulting from the peak standing crop analysis was determined by means of nitrogen analyses according to Kjeldahl (Siegel 1976).

To get an impression of the amount of grazed phytomass, immediately after grazing the grazing-leftover of the plot adjacent to the mini-exclosure and of the same size (1 x 2 m) was mown, dried and weighed in the same manner as the ungrazed plots. The percentage of grazed phytomass on each plot was calculated as: $100\ \% * [\text{phytomass}_{(\text{ungrazed plot})} - \text{phytomass}_{(\text{grazed plot})}] / \text{phytomass}_{(\text{ungrazed plot})}$. Before the experiment started, the similarity of the two adjacent plots was proved by relevés of each plot.

Statistical analyses

For the statistical examination of correlations, Spearman's rank correlation coefficients were calculated by means of STATISTICA 6. For the validation of the methods, we used a

hyperbolic regression. Correlation coefficients (r_S) and coefficients of determination (r^2) that are significant on a level of $p < 0.05$ are marked with *, on a level of $p < 0.01$ with ** and in the case of $p < 0.001$ with ***.

To test for differences among the three investigated years and the vegetation types as well as an interaction between year and vegetation type, mixed linear models were calculated (SAS 8.02, Proc Mixed). These models are especially suited for analysing repeated-measure data (Littell et al. 1998), because they allow comparison of the goodness of fit of several covariance structures. We tested autoregressive (1), heterogeneous autoregressive (1), autoregressive moving averages (1,1), unstructured, compound symmetry and Huynh-Feldt and chose the one with the best Akaike (AIC) values for the final calculations. Post hoc multiple comparisons were Tukey-adjusted.

Results

Validation of the methods of analysing productivity

Figure 4.2 shows the correlation between the peak standing crop analyses and the CIR approach for the years 2000 and 2001. In both years there is a highly significant correlation between the two methods. The relationship can be described best by a hyperbolic regression. The curve approaches a maximum value of 175 or 222, respectively. This can be explained by the specifics of the red value factor, which has a maximum at 255. But altogether the regression shows that especially for our slightly and moderately productive plots, where red values are low to intermediate, the two methods correspond very well and highly significantly.

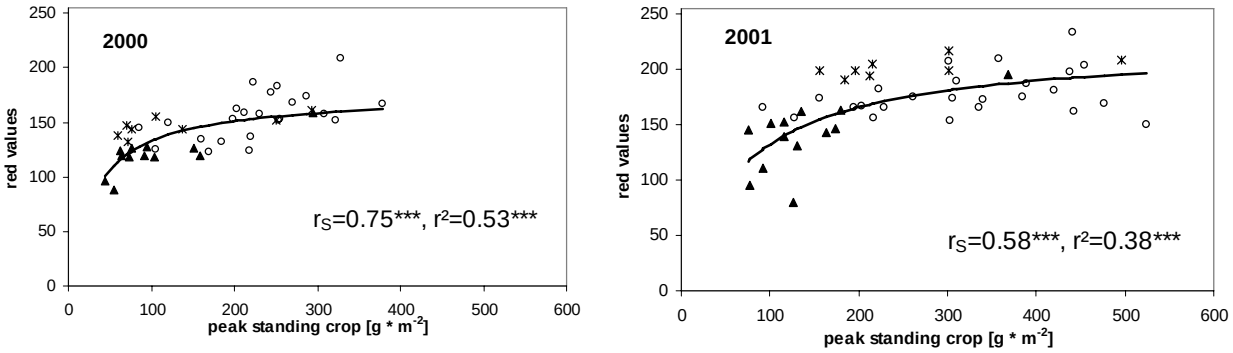

Figure 4.2. Correlation between peak standing crop and red values of the plots in the years 2000 and 2001. Hyperbolic regression 2000: red values = (175.44 x peak st. crop) / (32.07 + peak st. crop). 2001: red values = (222.22 x peak st. crop) / (67.91 + peak st. crop). ▲: plots belonging to the K-vegetation type, ✳: plots belonging to the F-vegetation type, O: plots belonging to the A-vegetation type.

Differences among the years and the vegetation types

The average values of all variables are given in Table 4.1. For all investigated variables there are significant differences among the years. In case of the peak standing crop, all three years are different from each other; for the other variables two of the three years differ (see Table 4.1). Peak standing crop was highest in 2001 whereas species number, number of endangered species and crude protein content were highest in 2000. The percentage of grazed phytomass was lowest in 2002, when the new grazing regime was established. The red values cannot be compared between different dates of flight because they are dependent on the weather conditions.

fine-grain scale	year	K	F	A	complete	p (year)	p (paddock type)	p (paddock*year)
n		13	8	25	46			
species number	2000	17.1 (0.61)	14.8 (1.49)	15.7 (0.53)	15.8 (0.43) a	0.0023	0.0036	n.s.
	2001	16.9 (0.87)	12.9 (0.40)	13.7 (0.66)	14.5 (0.52) b			
	2002	16.0 (0.7)	12.1 (1.13)	15.4 (0.42)	14.5 (0.42) b			
	mean	16.7 (0.42) a	13.3 (0.65) b	14.9 (0.35) c				
number of red data species	2000	2.5 (0.29)	1.8 (0.31)	1.7 (0.20)	2.0 (0.15) a	0.0239	<0.0001	0.008
	2001	2.5 (0.31)	1.3 (0.16)	1.0 (0.20)	1.6 (0.18) b			
	2002	2.9 (0.19)	1.1 (0.30)	0.9 (0.14)	1.6 (0.17) b			
	mean	2.6 (0.16) a	1.4 (0.16) b	1.2 (0.12) b				
peak standing crop [g m^{-2}]	2000	105.8 (20.00)	133.2 (31.72)	227.3 (15.04)	154.9 (14.1) a	<0.0001	<0.0001	0.038
	2001	142.8 (20.99)	257.8 (38.84)	317.1 (21.28)	239.2 (18.9) b			
	2002	82.9 (9.95)	208.5 (37.55)	320.6 (29.09)	208.5 (23.2) c			
	mean	111.4 (10.87)a	199.8 (22.6) b	287.0 (14.11) c				
red values	2000	119.2 (4.73)	146.6 (3.30)	155 (4.20)	143.4 (3.53) a		<0.0001	
	2001	139.8 (8.35)	201.6 (2.98)	177.6 (3.78)	171.1 (4.52) b			
	mean	129.5 (5.14) a	174.1 (7.42) b	166.3 (3.30) b				
crude protein content [%]	2000	8.7 (0.39)	9.3 (0.85)	9.6 (0.34)	9.2 (0.26) a	0.0343	n.s.	n.s.
	2001	8.4 (0.36)	8.6 (0.70)	8.8 (0.38)	8.5 (0.28) b			
	2002	8.1 (0.30)	7.0 (0.63)	9.6 (0.42)	8.5 (0.31) ab			
	mean	8.4 (0.20) a	8.3 (0.46) a	9.3 (0.23) a				
grazed phytomass [%]	2000	46.7 (4.25)	31.3 (5.70)	35.2 (3.67)	37.7 (2.63) a	0.0027	0.0234	0.001
	2001	35.4 (4.23)	40 (6.81)	48.9 (3.90)	41.5 (2.96) a			
	2002	9.8 (4.16)	25.6 (8.95)	43.3 (5.82)	26.0 (4.25) b			
	mean	30.8 (3.47) a	32.3 (4.20) ab	42.6 (2.68) b				

broad scale		K	F	A	complete
n		17	8	18	43
species number	2001	44.3 (1.33)	37.4 (1.67)	39.9 (1.36)	42.0 (0.89)
number of red data species	2001	5.9 (0.27)	4.3 (0.41)	3.1 (0.34)	4.4 (0.27)
red values	2001	128.7 (6.02)	183.3 (4.24)	174.5 (4.53)	158.0 (4.80)

Table 4.1. Mean values of the variables for the three investigated years and the three paddocks. The standard error is given in parentheses. n: number of observations, a,b,c: average values that are marked with different letters are significantly different, p: level of significance (mixed linear model, SAS, proc mixed).

Concerning the three vegetation types (K, F, A), species number and the number of endangered species were highest for the Koelerion glaucae vegetation type at the fine-grain scale as well as at the broad scale. Conversely, peak standing crop and red values at the fine-grain scale as well as red values at the broad scale were lowest for these Koelerion glaucae communities. Accordingly, the percentage of grazed phytomass was also lowest at these plots. There is no significant difference between the vegetation types with respect to the crude protein content. The number of endangered species, peak standing crop and grazed phytomass

show significant interactions between vegetation type and years, which means that differences between the vegetation types are dependent on the year.

On both scales the relationships between the vegetation types are very similar, although species number as well as the number of endangered species are about 2-3 times higher at the broader scale than at the fine-grain scale.

Relationships between the investigated variables

At the fine-grain scale (2 m², Figure 4.3) there is in 2000 and 2002 no significant rank correlation between peak standing crop and species number. In 2001 there is a highly significant negative correlation. This is due to a decline in species number in the more productive plots of the Armerio-Festucetum trachyphyllae vegetation type (Table 4.1).

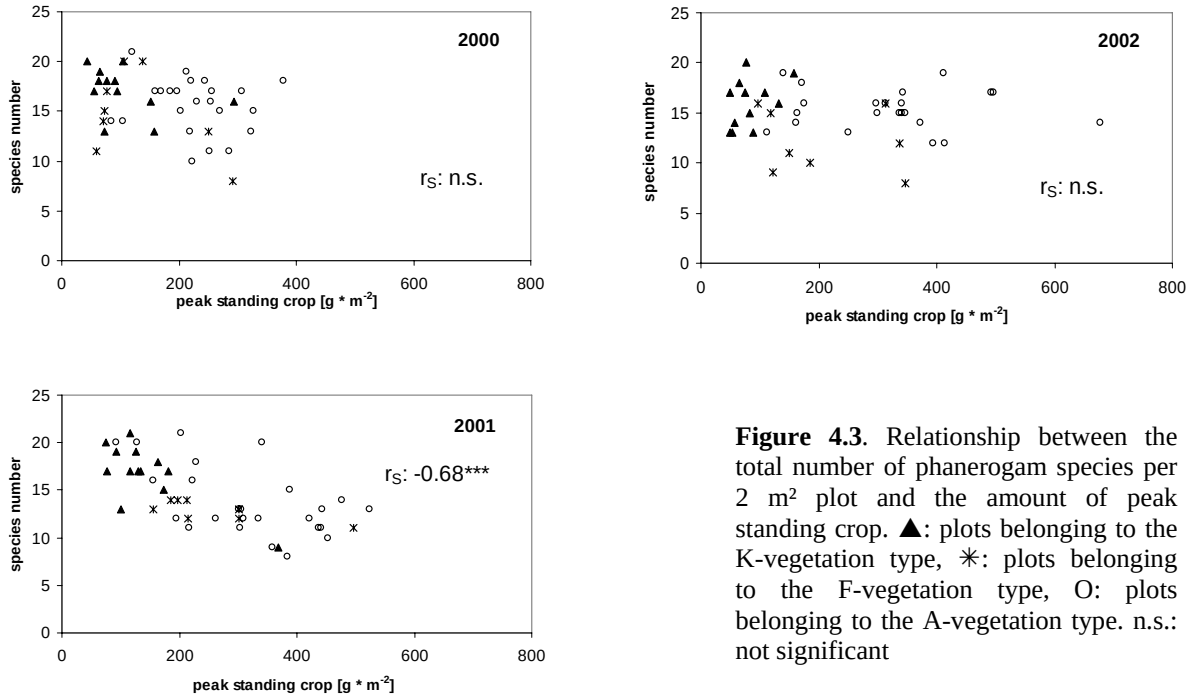

Figure 4.3. Relationship between the total number of phanerogam species per 2 m² plot and the amount of peak standing crop. ▲: plots belonging to the K-vegetation type, ✳: plots belonging to the F-vegetation type, O: plots belonging to the A-vegetation type. n.s.: not significant

The CIR approach produced the same result (Figure 4.4a): no correlation in 2000 and a negative rank correlation between red values and species number in 2001. At the broader scale of the grid plots (79 m², Figure 4.4b) the relationship between red values and species number was unimodal. It can be described by a quadratic regression curve. Highest species numbers (40-50) are reached on plots with medium red values, which are associated with comparatively “productive” Koelerion glaucae plots or rather “unproductive” Armerio-Festucetum trachyphyllae plots. The plots at the left margin with low red values are characterised by lower species numbers. These are the plots which are very sparsely covered

with vascular plants (< 40 %) but have a high cover of bryophytes. They are pioneer Koelerion glaucae stages.

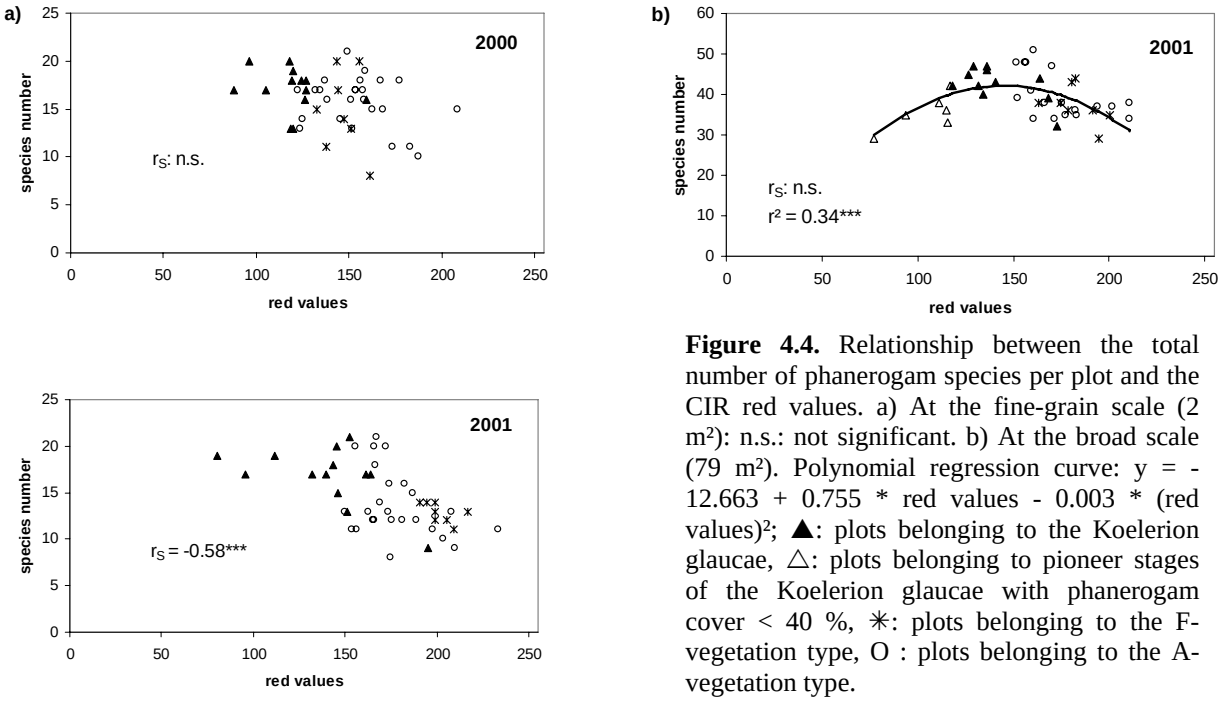

Figure 4.4. Relationship between the total number of phanerogam species per plot and the CIR red values. a) At the fine-grain scale (2 m²): n.s.: not significant. b) At the broad scale (79 m²). Polynomial regression curve: y = -12.663 + 0.755 * red values - 0.003 * (red values)²; ▲: plots belonging to the Koelerion glaucae, △: plots belonging to pioneer stages of the Koelerion glaucae with phanerogam cover < 40 %, ✳: plots belonging to the F-vegetation type, O : plots belonging to the A-vegetation type.

The differences between the pioneer and the grassland Koelerion glaucae stages are shown in Table 4.2. At both scales, productivity is lower in the pioneer stages, as shown by the red values and cover of vascular plants at both scales as well as with peak standing crop at the fine-grain scale. In accordance with these results the crude protein content of the phytomass and the amount of grazed phytomass at the fine-grain scale are also lower in case of the pioneer stages. But there is a marked difference between the scales in the case of the species number. Whereas at the fine-grain scale species number is highest on the pioneer plots, at the broad scale it is much higher on the Koelerion glaucae grassland than on the Koelerion glaucae pioneer plots. In the case of the endangered species, at the broad scale there is no difference between the communities, whereas at the fine-grain scale the number of endangered species is slightly higher for the pioneer stages.

fine-grain scale	year	K pioneer	K grassland
n		2	11
peak standing crop [g m^{-2}]	2000	49 (23.51)	117.1 (22.37)
	2001	101.7 (75.22)	150.3 (32.08)
	2002	61.1 (3.06)	87.3 (11.51)
red values	2000	92.2 (45.11)	124.1 (3.98)
	2001	87.8 (13.37)	149.3 (5.70)
species number	2000	18.5 (8.25)	16.8 (0.67)
	2001	18.0 (2.32)	16.6 (0.99)
	2002	16.0 (2.00)	16.0 (0.79)
number of red data species	2000	3.5 (0.75)	2.3 (0.30)
	2001	3.5 (0.70)	2.4 (0.30)
	2002	3.0 (0.00)	2.9 (0.23)
crude protein content [%]	2000	6.9 (2.45)	9.1 (0.37)
	2001	6.8 (1.35)	8.7 (0.58)
	2002	6.8 (0.45)	7.5 (0.33)
grazed phytomass [%]	2000	40.2 (19.12)	48.0 (4.54)
	2001	17.4 (13.79)	38.7 (5.88)
	2002	9.1 (9.14)	10.0 (4.85)
cover of phanerogams [%]	2000	57.5 (2.5)	58.2 (4.87)
	2001	50.0 (0.0)	63.6 (6.88)
	2002	50.0 (0.0)	62.0 (2.91)
broad scale			
n		6	11
red values	2001	105.0 (6.56)	141.66 (5.52)
species number	2001	35.5 (1.86)	42.5 (1.32)
number of red data species	2001	5.8 (0.31)	5.9 (0.39)
cover of phanerogams [%]	2001	31.7 (2.11)	58.6 (3.38)

Table 4.2. Mean values of the variables for two different communities of the Koelerion glaucae vegetation complex. The standard error is given in parentheses. n: number of observations.

At the fine-grain scale the relationship between the number of endangered species and peak standing crop (Figure 4.5) is significantly negative in all investigated years, especially in 2001.

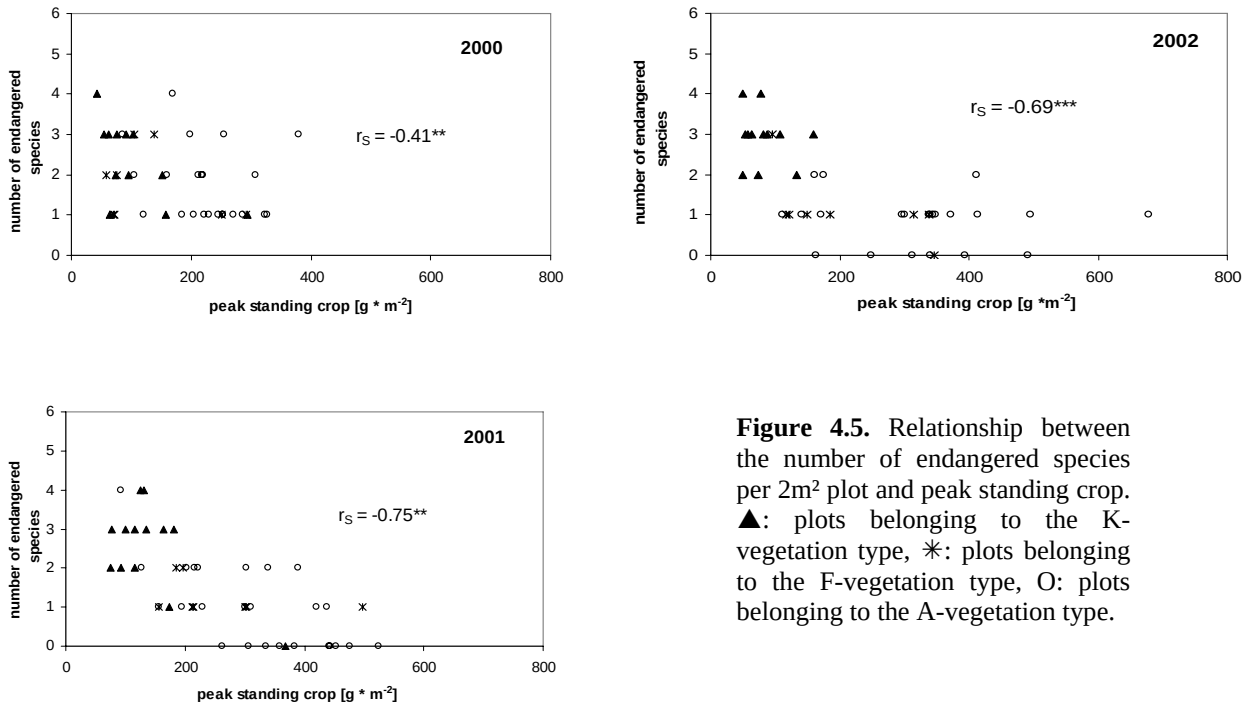

Figure 4.5. Relationship between the number of endangered species per 2m² plot and peak standing crop. ▲: plots belonging to the K-vegetation type, ✳: plots belonging to the F-vegetation type, O: plots belonging to the A-vegetation type.

The same is true if the red values are used as a measure for productivity (Figure 4.6a). At the broader scale the relationship is also negative and highly significant (Figure 4.6b). In all cases there are fewer endangered species on plots with higher productivity.

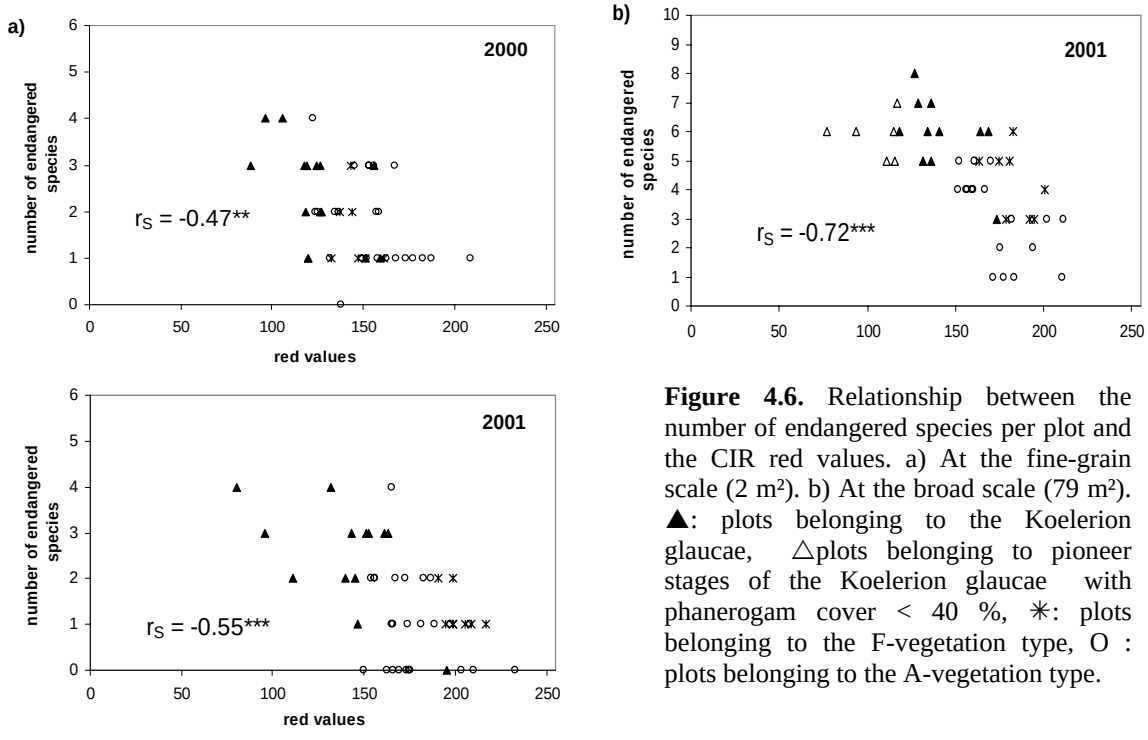

Figure 4.6. Relationship between the number of endangered species per plot and the CIR red values. a) At the fine-grain scale (2 m²). b) At the broad scale (79 m²). ▲: plots belonging to the Koelerion glaucae, △plots belonging to pioneer stages of the Koelerion glaucae with phanerogam cover < 40 %, ✳: plots belonging to the F-vegetation type, O : plots belonging to the A-vegetation type.

Rank correlations between crude protein content and peak standing crop (Figure 4.7, and also between crude protein content and red values, not shown) were used to test whether more productive plots are characterised by higher nitrogen content. The relationship is positive throughout all investigated years and both independent variables (see Figure 4.7; regarding the red values: 2000: $r_S = 0.43^{**}$, 2001: $r_S = 0.47^{**}$).

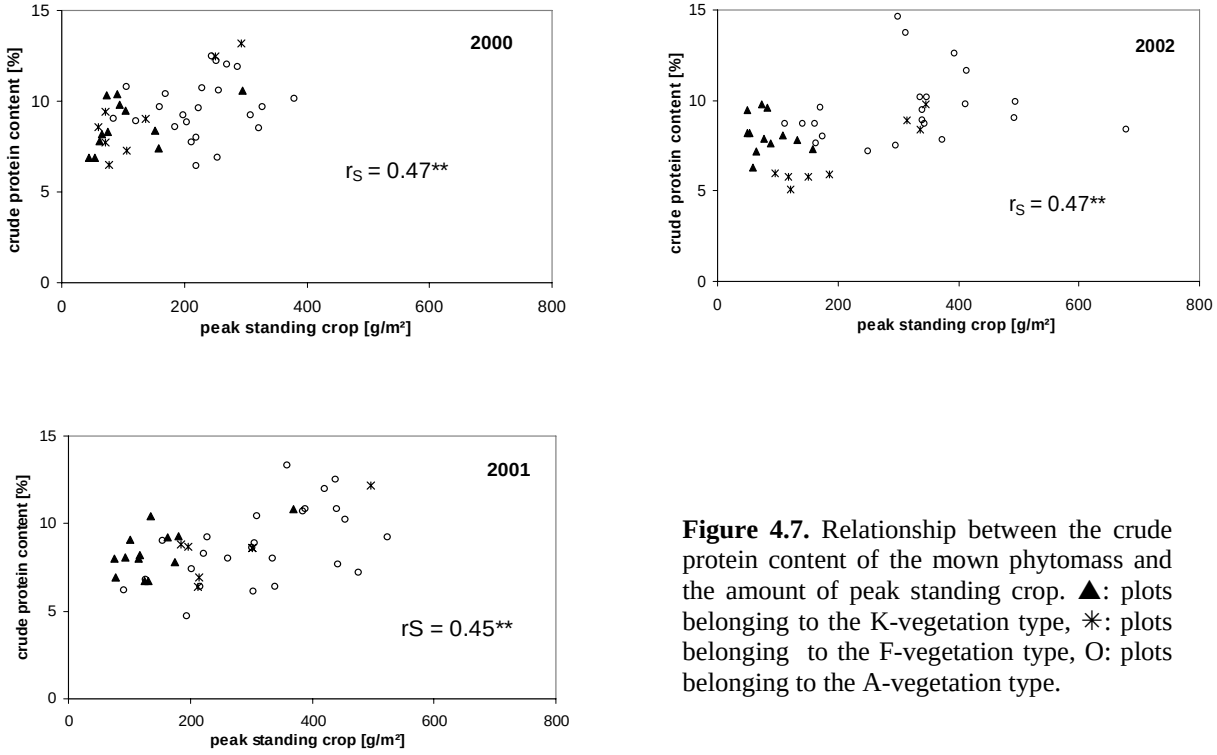

Figure 4.7. Relationship between the crude protein content of the mown phytomass and the amount of peak standing crop. ▲: plots belonging to the K-vegetation type, ✳: plots belonging to the F-vegetation type, O: plots belonging to the A-vegetation type.

The relationships between grazed phytomass and crude protein content (not shown) on the one hand as well as between grazed phytomass and peak standing crop (Figure 4.8) on the other are not significant in 2000, weakly significant in 2001 and highly significant in 2002 (see Figure 4.8; regarding grazed phytomass versus crude protein content: 2000: not significant., 2001: $r_S = 0.31^{*}$, 2002: $r_S = 0.54^{***}$). The main difference is that in 2002 many plots with low peak standing crop and low crude protein content remained virtually ungrazed.

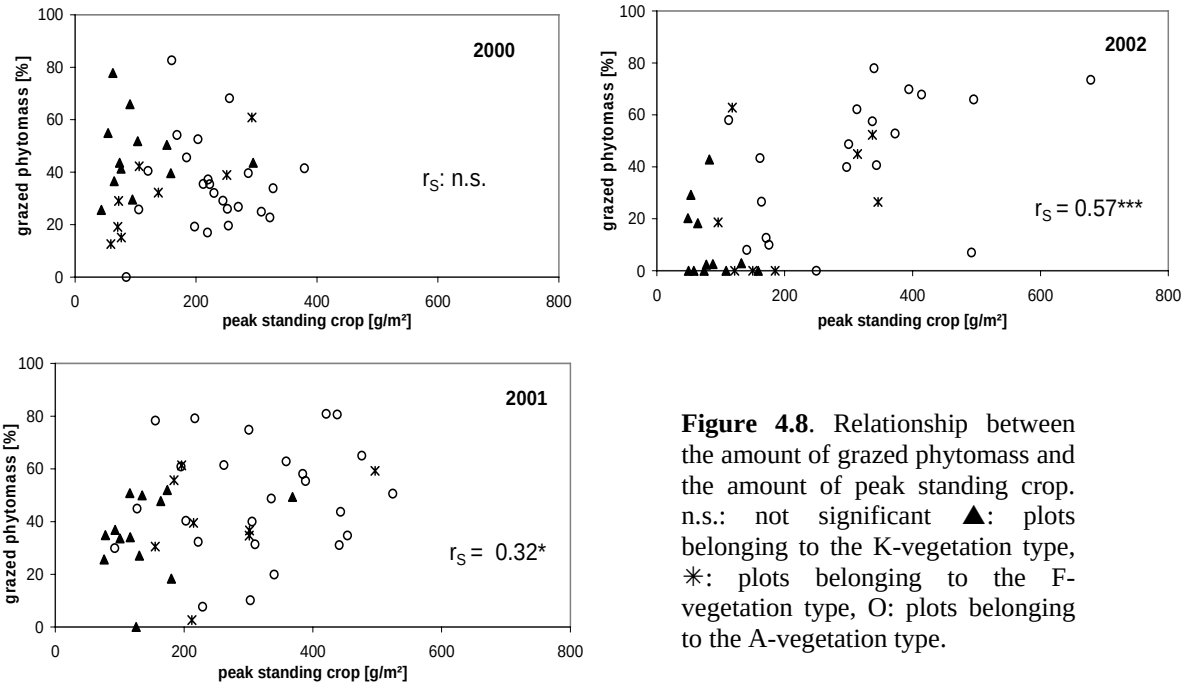

Figure 4.8. Relationship between the amount of grazed phytomass and the amount of peak standing crop. n.s.: not significant ▲: plots belonging to the K-vegetation type, ✳: plots belonging to the F-vegetation type, O: plots belonging to the A-vegetation type.

Discussion

Comparing the methods of measuring "productivity"

The two applied methods of estimating productivity show a highly significant correlation. Additionally, the correlation with species number, number of endangered plant species and crude protein content on the one hand and peak standing crop as well as red values as independent variables on the other hand are also very similar at the fine-grain scale. Hence, the two methods are compatible. The CIR imaging approach is a suitable method of obtaining productivity data for large areas without the need to disturb the area by clipping.

Integrating the data into a general gradient

The investigated ecosystem is characterised by comparatively high numbers of vascular plant species and a rather high abundance of endangered plant species.

Productivity is very low; the mean amount of peak standing crop is about 25 % of that of a meadow managed with average intensity (Mährlein 2004) and hardly fits within the lowest values of the "normal range" of temperate grassland, 200-5000 g * m^{-2} (Whittaker 1970). So considering the broad ecological amplitude, our investigation area can be classified as a low-productivity to extremely low-productivity type.

The mean crude protein content of the phytomass is also very low. At many plots crude protein content falls short of the limit of 9 %, beyond which an additional food ration is necessary for livestock nutrition (Mährlein 2004). Optimal crude protein content for sheep

grazing is set between 16 and 20 % (N.N. 2004). In our case, extensive sheep breeds (Skudde, Rhoen sheep, Moorschnucke) are used as grazing animals, thus they are able to cope with low-productivity grassland. Nevertheless additional food resources are necessary to guarantee adequate animal nutrition in the long run.

The differences among the vegetation types emphasise the productivity and diversity gradient along the investigated area where the pioneer Koelerion glaucae stages differ from denser Armerio-Festucetum grassland. The differences among the investigated years and the fact that some relationships are only significant in certain years is probably due to a variation of abiotic factors, e.g., the precipitation rate. So our results demonstrate that it is important to analyse several years. A strong influence of the annual precipitation rate on productivity has already been pointed out by Whittaker (1970). This factor has been used in numerous studies as a model variable of productivity (e.g. Abramsky & Rosenzweig 1984).

The importance of scale

The results of the investigation give a basis for developing a model which combines ecological and economical aspects concerning plant species richness, productivity and livestock nutrition for our model system. Figure 4.9 shows a schematic diagram of the interrelationship of the investigated factors for both scales.

Figure 4.9 points out the different relationships between the investigated variables and the vegetation type, e.g., the gradient from pioneer stages to dense grassland at the fine-grain (a) and broader scale (b). While the relationships between the vegetation gradient and red values as well as the number of endangered plant species are more or less identical at both scales, there is a strong impact of scale on the results regarding plant species richness: at the broader scale, species number is lower for pioneer Koelerion glaucae stages than for dense Armerio-Festucetum grassland and is highest for intermediate stages, while at the fine-grain scale, species richness decreases continuously. In contrast, Roscher et al. (2005) and Allock & Hik (2003) found the same shape of response curve when they analysed the relationship between plant species richness and standing crop at two different scales. But as their investigation sites were experimental grassland communities and Australian woodland, respectively, the impact of scale can be completely different in our system.

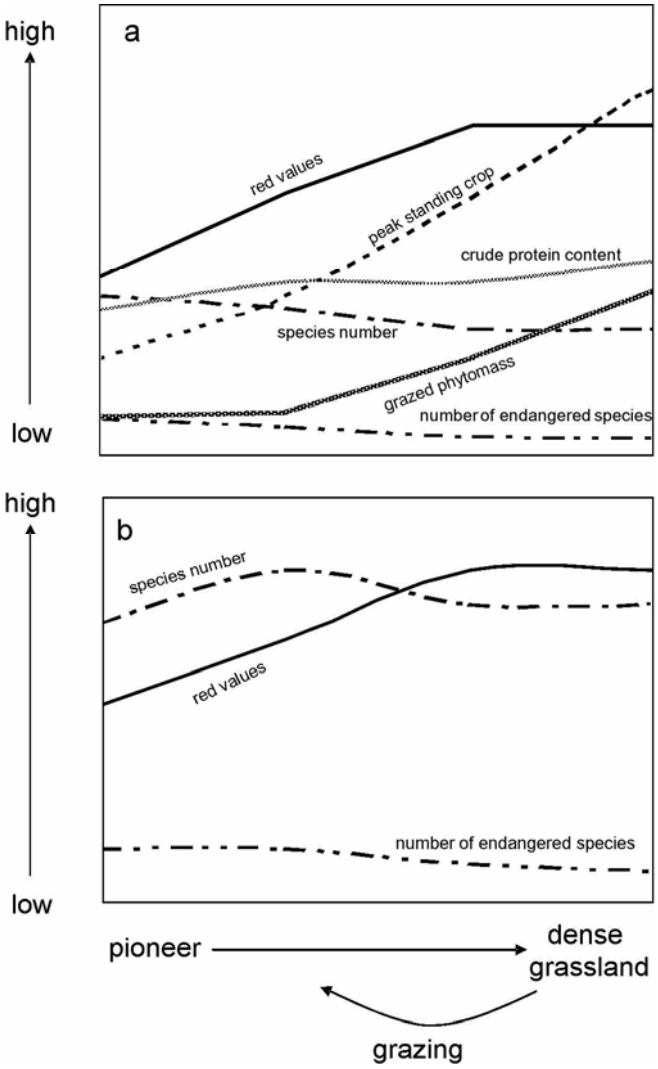

Figure 4.9. Conceptual model for the interrelationship between the variables along a vegetation gradient from pioneer (Koelerion glaucae) to dense grassland communities (Armerio-Festucetum trachyphyllae) a: At the fine-grain scale. b: At the broad scale. The scaling of the axes is congruent in both diagrams. low/high: increasing intensity of the concerned variables from low to high intensity.

A comparison between Figures 4.4a and 4.4b shows that one possible explanation of the different relationships at the two scales is that at the fine-grain scale, failure to achieve maximum plant species richness is due to a limited plot size. This possible artefact has already been discussed by Oksanen (1996), who suggested that on plots with higher productivity, plant species richness can be limited by plot size. Altogether, our results strongly emphasise the importance of scale for diversity studies.

Plant species richness-productivity relationships

The question of a general relationship between plant species richness and productivity has been intensively discussed during recent decades. Most often favoured is the model of a unimodal hump-shaped relationship as proposed by Grime (1973) (e.g. Tilman 1982,

Abramsky & Rosenzweig 1984, Rosenzweig 1992, García et al. 1993, Tilman & Pacala 1993, Huston & De Angelis 1994). But depending on the system, positive correlations have also been described, e.g., for Mediterranean shrubland (Troumbis & Memtsas 2000) or experimental grassland communities (Pfisterer et al. 2004, Roscher et al. 2005), while negative relationships were proposed for fertilisation experiments (Tilman et al. 1996, Rajaniemi 2003). The humped relationship and comparable models (e.g. Beierkuhnlein & Jentsch 2005) apply over a large ecological amplitude ranging from very low to high productivity. Considering the whole ecological amplitude, our investigation area with nutrient-poor sand grassland can be integrated into the ascending part of the hump-shaped model, so we should expect a positive relationship between diversity and productivity. But on the contrary, at the broad scale we found decreasing species numbers if peak standing phytomass exceeds ca. 150 g * m^{-2}, which is a very low value (see Figure 4.4b, 2). From early to mid-successional stages, a negative relationship between plant species richness and productivity is detected. Only the extremely open pioneer plots in the Koelerion glaucae complex with low cover of vascular plants are characterised by lower species numbers.

Other authors who detected a negative relationship (e.g. Tilman et al. 1996, Gough & Grace 1998, Gough et al. 2000) either investigated highly productive areas or performed experiments with nitrogen applications, where the availability of species is probably not guaranteed (Gough et al. 2000). Kahmen et al. (2005) investigated rather productive Geranio-Trisetetum plots in montane European grasslands but found no relationship between plant species richness and productivity; instead there was a strong relationship between floristic plant community composition and productivity at the fine scale (2 m x 2 m).

Very recently an intensive debate has arisen regarding the phenomenon of overyielding, the situation in which production in plant mixtures exceeds expectations based on monoculture yields (e.g. Hooper & Dukes 2004, Roscher et al. 2005). This effect can depend on the functional characteristics of the species and biotic and abiotic parameters (Hooper & Dukes 2004) and is typical for “experimental plant communities”. Our results demonstrate that in natural low-productivity communities the relationships likewise depend on annual variations of abiotic, e.g., climatic conditions. But the result for our system is completely different and overyielding can not be expected for these low-productivity plant communities.

According to Aarssen (2001) the heterogeneity of the environment, the opportunity for facilitation and the availability of species are important for species richness and cause the hump-shaped curve between species richness and productivity. In our case, the investigation area is a sheep-grazed habitat where heterogeneity is higher and gaps are easily created by the

grazing animals. According to Fynn et al. (2004) and Lepš (2005), disturbance may be an important determinant of diversity by modifying resource availability and the abundance and vigour of competitive dominants. Other authors, too, have stated that disturbance may influence productivity and can reduce the intensity of competition for a limiting resource (Wilson & Tilman 1993).

The availability of species, also mentioned by Aarssen (2001) as a reason for the humped relationship, is probably not a limiting factor in our investigation area. The seed-bank is rich in species and even contains threatened species such as *Phleum arenarium* or *Medicago minima* (Eichberg et al. 2006). Additionally there is epi- and endozoochoric seed dispersal by sheep (Eichberg et al. 2005).

Although there have been many investigations on this subject, "what controls the loss of species along both natural and experimental productivity gradients remains unknown" (Mittelbach et al. 2001). This leads to the conclusion that there is no universally valid relationship between productivity and plant species richness, but that the kind of correlation mainly depends on the system. This is supported, e.g., by a comparison of the positive scale-independent relationships in experimental Arrhenatherion communities (Roscher et al. 2005) and the negative, scale-dependent relationship of our low-productivity Koelerio-Corynephoretea system.

Concerning the negative relationship between productivity and the number of endangered plant species, one explanation may be that rare species are often specialised for nutrient-poor conditions. This emphasises the need of adequate management methods such as grazing to prevent nutrient enrichment and grass-encroachment.

Livestock diet and plant species richness

Since in the model system one aim of nature conservation is to protect and develop a high diversity of site-specific plant species, the optimal relationship between ecological and economical purposes would be that sites with the highest productivity and the highest value for animal nutrition are the ones with the highest diversity of site-specific plant species.

The results have shown that the more productive plots are characterised by higher crude protein contents and therefore are more attractive to the grazing animals. This correlation has been shown by other authors for old fields in Canada (Bonser & Reader 1995), and for managed savanna systems (Augustine et al. 2003).

This has consequences for the grazing intensity in that (with the modified grazing regime in 2002) grazing intensity is high at plots with high productivity and low plant species richness,

and low at plots with low productivity and high plant species richness. Other studies in the same investigation area have shown that grazing causes a regression towards pioneer stages with lower productivity, which is expressed by lower cover of vascular plants (Süss et al. in prep.). As a consequence, these habitats are not self-maintaining in the long run because on the one hand grazing is essential for their existence while on the other hand, sheep need an additional food resource. So one important conclusion of this investigation is that in our mainly low-productivity model system there is a dilemma between plant species richness and livestock nutrition, i.e. between ecological and economical aspects.

Conclusions for the management of threatened sand ecosystems

The combination of the two factors - low productivity and low crude protein contents of the plants - emphasises that a satisfactory livestock nutrition cannot be guaranteed if there is no additional food resource. But on the other hand “diversity (of grasses) expands the period of adequate forage quality...” (Ganskopp & Bohnert 2001) and in that case is also important for a varied nutrition. In view of the need for adequate grazing management according to targets of nature preservation, which we have already pointed out, an optimal combination would be that sheep can graze in alternation between these described low-productivity areas: a) with a nutrient-poor but varied diet and b) more productive nutrient-rich areas with low plant species richness, where adequate livestock nutrition is guaranteed. In this case nutrient transfer between b) and a) must be prevented, because the specific structure of a) depends on the nutrient-poor conditions. This concept is the central aspect of a “Testing and Development” project funded by the “Federal Agency for Nature Conservation” (Germany) from 2004 to 2008.

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Chapter 5:
Diet preferences of sheep and donkeys as a tool for the management of threatened sand ecosystems?

Abstract

Extensive grazing has turned out to be an important tool for managing fallow grassland in order to restore ecosystems with formerly high phytodiversity. Ruminants and non-ruminants should have different impacts, e.g. for the management of grass-encroachment. We investigated a dry and nutrient-poor primary calcareous sand ecosystem located in the Upper Rhine Valley (Germany) as a model system. Local sheep breeds (as a model for ruminants) and donkeys (as a model for non-ruminants) were used as grazing animals. Additionally, we investigated the impact of successive combination of both animal species. Two different vegetation types (each threefold replicated) were each grazed once a year for a short period. In 2003 and 2004 the effects of the three treatments (sheep grazing, donkey grazing and successive two-species grazing) on phytomass extraction were investigated in a field experiment, which was stratified for two vegetation types. The weighed phytomass of the grazing-leftover on 2-m² plots was compared with that on ungrazed mini-exclosures of the same size, differentiated into the three plant functional types (PFTs) graminoids, Fabaceae and other herbs.

The maximum phytomass extraction was achieved with the two-species approach, although the quantitative phytomass extraction by sheep and donkeys was not significantly different. Sheep extract more phytomass of herbs than of graminoids, whereas donkeys select for Fabaceae. With the two-species treatment all PFTs were grazed to the same degree.

Sheep grazing cannot reduce phytomass with relatively high fibre content to the same degree as donkey grazing. The successive combination of ruminants and non-ruminants is an ideal method for the reduction of grass-encroachment and to achieve maximum phytomass extraction, and thus to restore and to preserve high phytodiversity.

Introduction

During recent years, extensive grazing has turned out to be an important tool for fallow grassland management with the aim of restoring ecosystems with formerly high phytodiversity (e.g. Kooijman & van der Meulen 1996, Hellström et al. 2003, Schwabe et al. 2004, Pykälä et al. 2005). Depending on the ecosystem type, different species of livestock are used for ecosystem management. Often ruminants, in most cases cattle or sheep but sometimes also goats, are of importance. In other cases, non-ruminants, especially equids are used as grazing animals. Whereas the feeding behaviour of equids is thought to be characterised by large intakes with low nutrient extraction (Mueller et al. 1998), ruminants are said to possess a certain degree of "nutritional wisdom" (Ngwa et al. 2000), while sheep diets are even more variable than cattle diets (Grant et al. 1985). Recently traditional multi-species grazing with a combination of ruminants and non-ruminants has also been considered as a tool of ecosystem management (e.g. Menard et al. 2002, Loucougaray et al. 2004, Süss 2004, Lamoot et al. 2005a). In these cases, ruminants and non-ruminants are most often represented by cattle and horses for management of wet or moist ecosystems. Due to morphological and physiological differences between the species, e.g. the structure of the incisor arcade or different digestive systems, differences in foraging behaviour and habitat use are expected (Lamoot et al. 2005a).

In this study, we focus on inland sand ecosystems on calcareous sandy sites. As these ecosystems are characterised by rather dry and nutrient-poor conditions, local sheep breeds (Skudde, Moorschnucke, Rhoen sheep) are especially suitable as grazing ruminants. Sheep are able to select for nutrient-rich plants on paddocks that are characterised by lower mean nutrient-values (Jeroch et al. 1999). The ability to cope with a nutrient-poor diet depends on the sheep breed (Bartolomé et al.1998, Jeroch et al. 1999). Sheep grazing is often used for nature conservation and has proved to be an adequate management method (Jeroch et al. 1999, Hellström et al. 2003).

Especially in case of more ruderal sites with a high abundance of tall competitive grass species, equids have come into use as grazing animals for the management of these habitats. As hindgut fermenters equids are better than ruminants at digesting a diet with high fibre content. In view of the nutrient-poor conditions of the investigated ecosystem, we chose donkeys for the management of these habitats. Donkeys are especially well adapted to dry and nutrient-poor ecosystems, reflecting their origin in a hot semi-arid environment (Pearson et al. 2001). Lamoot et al. (2005b) recently stated that donkeys are sufficiently well nourished by

the scarce vegetation of coastal sand ecosystems and might play a major role in nature management, especially in ecosystems with low forage quality. As yet there are only a few studies on donkeys as grazing animals (e.g. Aganga & Tsopito 1998, Canacoo & Avornyo 1998, Aganga et al. 2000, Lamoot et al. 2005b) and no study has been done in a comparable, primarily calcareous inland sand ecosystem.

Regarding the agroeconomical context, sheep in our investigation area are integrated in a system of direct marketing of high-quality meat from nature protection areas (Mährlein 2004), while donkeys are mainly used for breeding purposes and to assist public relations of a nature protection association.

We studied phytomass extraction and preferences on the basis of the plant functional types (PFTs) “graminoids”, “Fabaceae” and “other herbs” for both single-species grazing (sheep or donkey) and multi-species grazing, in our case two-species grazing (sheep and afterwards donkeys). As far as we know, no comparable quantitative study in a high-phytodiversity ecosystem has yet been published.

Plant species composition and thus grazing preferences may be different in different years - for instance, according to climatic conditions (Fahnestock & Detling 1999). Additionally, especially equids have a different foraging behaviour if they graze the same paddock several times, because they tend to avoid faeces-accumulation sites (Bogner & Grauvogl 1984). Therefore, and due to the impact of the annual differences in precipitation regime, the study was repeated in two successive years (2003 and 2004).

The main questions are:

- How is the “floristic background” of the high-phytodiversity system characterised, which species are grazed, which are rejected by the grazing animals?
- How much phytomass is grazed in the case of sheep grazing, donkey grazing and sheep followed by donkey grazing?
- Which PFTs are selected by sheep and donkeys and how intense is the phytomass extraction of these PFTs in case of the two-species treatment?
- Are there different results depending on the year of investigation?
- What conclusions follow for the management of low-productivity, threatened ecosystems?

Materials and methods

Study area

The investigation took place in the years 2003 and 2004 in the northern Upper Rhine Valley (Germany) about 30 km south of Frankfurt/Main (Hesse) near Darmstadt. A nature reserve ("Ehemaliger August-Euler-Flugplatz"), 71 ha in size, served as a model area for grazed inland sand ecosystems. The substrate is drifted sand which had been blown-out from calcareous Rhine deposits during late glacial and post-glacial periods. Especially in the eastern part of the investigation area calcareous horizons are represented. In the western parts of the area primarily base-rich sands in the topsoil have been progressively acidified due to successional processes. The investigation site is characterised by plant communities belonging to the Armerio-Festucetum trachyphyllae and the floristically closely related *Festuca trachyphylla/duvalii*-community. Since 1999, the whole area has been grazed by sheep as a management tool against grass-encroachment and succession (Schwabe et al. 2002). Donkey grazing started in 2002 and successive two-species grazing (sheep and afterwards donkeys) in 2003.

The weather conditions in the two investigated years were very different. As the grazing period of the investigated paddocks always finished in August, the mean climate values from January to August of 2003 and 2004 are given. The mean temperature was 12.9 °C (data from Frankfurt/Main airport [Internet]) in 2003 and 11.7 °C in 2004 (long-term average for these months: 12.0 °C). Duration of sunshine was 1652 h, or 1239 h, respectively (long-term average: 1342 h) and the total precipitation reached 230 mm in 2003 and 410 mm in 2004 (long-term average: 390 mm). Thus 2003 was characterised by a very high duration of sunshine in combination with low precipitation rates in comparison to long-term average values, whereas 2004 was more or less an average year.

Grazing animals

Sheep and donkeys, as models for ruminants and non-ruminants, are well adapted to dry and nutrient-poor conditions. Due to the differences in their digestive systems, structure of the incisor arcade and metabolic requirements (Lamoot et al. 2005a) they are in different ways appropriate grazers of the investigated ecosystem. As hindgut fermenters equids are able to cope with a diet having a high fibre content (Jeroch et al. 1999) and can consume fibre at a faster rate than ruminants (Mueller et al. 1998). They are also better able than the ruminants to extract nutrients from grasses with very high fibre content (Menard et al. 2002). As is generally known, in contrast to ruminants, equids have upper and lower incisors and mobile

lips; thus they can graze close to the ground and consume short vegetation efficiently (Aganga & Tsopito 1998, Jeroch et al. 1999, Aganga et al. 2000). Sheep (Hafez 1962, Stroh et al. 2002, Hülber et al. 2005) as well as donkeys (Legel 1993, Mueller et al. 1998) are able to graze selectively, so that it is possible that the grazed areas include less preferred species. It is specific for equids that faeces-sites are not grazed (Bogner & Grauvogl 1984, Loucougaray et al. 2004). In the case of multi-species grazing with ruminants, this effect may be compensated (Jeroch et al. 1999).

Experimental design

The investigated area was stratified according to the two vegetation types mentioned above. In each of them 9 homogeneous paddocks of around 700 m² were chosen in accordance with the practicability of the grazing regime. The three treatments (sheep, donkeys, sheep followed by donkey grazing) were assigned to three paddocks each. Thus, the investigation was replicated thrice. Sampling was carried out in 2003 and 2004 on the same paddocks.

Grazing regime

Grazing took place during summer and involved about 500 sheep, or 2-3 adult donkeys and one foal. The sheep grazing regime was a dynamic one, in which small areas of about 1 ha - where the above-mentioned paddocks were integrated - were grazed once a year for 1or 2 days. The donkeys grazed the approximately 700 m² paddocks for about 3-5 days, depending on the amount of phytomass. In both cases, the paddocks were grazed as long as an adequate food supply for the animals could be guaranteed. In the case of the successive sheep and donkey grazing, at first the paddocks were grazed by sheep in the same manner as described above. But when sheep no longer found adequate food resources, the grazing-leftover of the sheep was subsequently grazed by the donkeys, in this case for about 1-2 days.

Phytomass sampling

To assess the percentage of grazed phytomass mini-exclosures (metal baskets) with an area of 2 m² were used. In each paddock 5 (2003) or 4 (2004) mini-exclosures were established prior to grazing. Their location was determined by evaluating how best to represent the various vegetational subtypes in the paddocks. The positions were different in the two years. At every ungrazed mini-exclosure plot and an adjacent complementary grazed plot of the same size, the vascular plant species were recorded by relevés according to the scale of Barkman et al.

(1964) before grazing took place. Cryptogams were not sampled by the harvest method (see below) and therefore not recorded. Nomenclature follows Wisskirchen & Haeupler (1998).
Immediately after grazing of each paddock, the ungrazed plots and the grazing-leftover on the grazed plots were mown by an electric clipper up to a stubble-field height of about 2 cm, and the phytomass - separated into the groups "graminoids" (including *Carex hirta*), "Fabaceae" and "other herbs" (without Fabaceae) - was dried for 48 h at 70 °C and afterwards weighed. PFTs with less than 10 g dry phytomass were not taken into account for the differentiated analysis. The percentage of grazed phytomass for each plant group as well as for the total phytomass of each plot was calculated as 100 % * [$phytomass_{(ungrazed\ plot)} - phytomass_{(grazed\ plot)}$] / $phytomass_{(ungrazed\ plot)}$. Additionally, the grazing preferences of the animals on the level of plant species were estimated: Immediately after grazing, the apparent grazing intensity was assessed by the modified scale of Stroh et al. (2002): not/hardly grazed (0 - 5 % of phytomass grazed), grazed (6 – 50 %) and intensively grazed (> 50 %).

Statistical analyses

The floristic structure of the plots was analysed by means of detrended correspondence analysis (DCA), calculated with PC Ord 4.0. Cover-abundance data were transformed to a 0 – 9 ordinal scale and the analysis was run with downweighting and rescaling of the axes, the number of segments being 26.
To analyse the effects of the factors "animal", "year", "vegetation type" and "plant functional type" on the phytomass extraction, mixed linear models were calculated (SAS 8.02, Proc Mixed), which are especially suitable for analysing repeated-measures data (Littell et al. 1998) because they allow comparison of the goodness of fit of several covariance structures. We tested autoregressive (1), heterogeneous autoregressive (1), autoregressive moving averages (1,1), unstructured, compound symmetry and Huynh-Feldt and chose the one with the best AIC values for the final calculations. The mean values and standard errors given here are those resulting from the Proc Mixed analysis. Post hoc multiple comparisons were Tukey-adjusted.

Results

Phytodiversity, floristic structure of the plots and grazing preferences on the species level

As 2003 was an extremely dry year, so that many therophytes were absent, the data for the "average" year 2004 were used for phytodiversity analysis and to demonstrate the "floristic background" of the plots. The number of vascular plant species per 2-m² plot was mostly

between 8 and 19 with a mean number of 11.4 (standard error [SE]: 0.3) consisting of 3.2 (SE: 0.1) graminoid species, 2.2 (SE: 0.1) Fabaceae and 5.9 (SE: 0.2) other herb species. In total, 58 vascular plant species were recorded, 51 in the Armerio-Festucetum vegetation type and 42 in the *Festuca trachyphylla/duvalii*-community vegetation type. Additionally, 6 cryptogam species (3 bryophytes and 3 lichens) were present.

The "floristic background" is demonstrated in Figure 5.1 by means of a DCA representing plots and plant species. The plots of the Armerio-Festucetum trachyphyllae sites (black) are situated at higher values on the first axis while the *Festuca trachyphylla/duvalii*-community plots (grey) are arranged at lower values. Those of the Armerio-Festucetum trachyphyllae type are more homogeneous than those of the *Festuca trachyphylla/duvalii*-community. At low values on the first and second axes, especially therophytes such as *Arenaria serpyllifolia* agg. or *Erodium cicutarium* agg. are characterised by high abundance, whereas at high values on the first or the second axes dominant grass species like *Elymus repens* or *Carex hirta* are more important. The plant species are marked with the median values of the grazing intensity in those cases with more than three observations. In total, 37 plant species are grazed or intensively grazed: 26 by donkeys (7 graminoid species, 4 Fabaceae and 15 other herbs) and 30 by sheep (8 graminoids, 6 Fabaceae and 16 other herbs). 20 plant species are grazed by both animals, which is an overlap of 54 %. The Red List species (according to Korneck et al. 1996) *Armeria maritima* ssp. *elongata, Medicago minima, Silene conica* and *Vicia lathyroides* are slightly more intensively grazed by sheep than by donkeys, whereas the dominant grass species *Elymus repens, Carex hirta, Poa angustifolia* and *Cynodon dactylon* are grazed by donkeys as well as by sheep. Although there are no data for sheep grazing on *Cynodon dactylon* from this study, our previous studies have shown that this plant species is grazed by sheep as well (unpublished data).

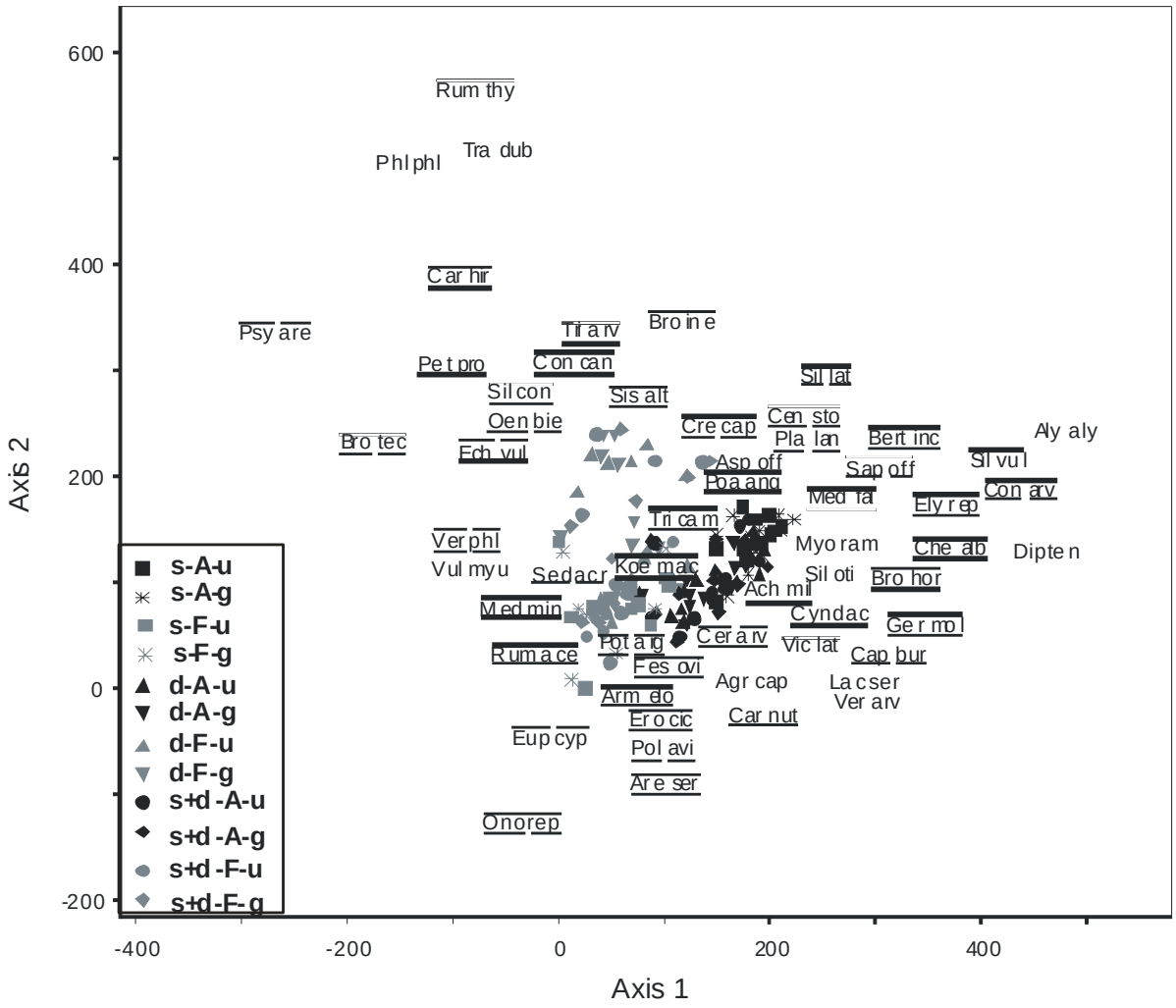

Figure 5.1. DCA of the investigated plots for the year 2004. Eigenvalues; length of gradients: first axis: 0.281; 2.21, second axis: 0.199; 2.44, third axis (not shown): 0.143; 2.42. s: sheep, d: donkeys, s+d: sheep followed by donkeys, F: *Festuca trachyphylla/duvalii*-community plots, A: Armerio-Festucetum trachyphyllae plots, u: ungrazed, g: grazed; Line above each plant species name: phytomass extraction by sheep, line below: phytomass extraction by donkeys. Interrupted line: not or hardly grazed (0 - 5 %), normal line: grazed (6 – 50 %), double-line: intensively grazed (> 50 %). Ach mil: *Achillea millefolium* agg., Agr cap: *Agrostis capillaris*, Aly aly: *Alyssum alyssoides*, Are ser: *Arenaria serpyllifolia* agg., Arm elo: *Armeria maritima* ssp. *elongata*, Asp off: *Asparagus officinalis*, Ber inc: *Berteroa incana*, Bro hor: *Bromus hordeaceus*, Bro ine: *Bromus inermis*, Bro tec: *Bromus tectorum*, Cap bur: *Capsella bursa-pastoris*, Car hir: *Carex hirta*, Car nut: *Carduus nutans*, Cen sto: *Centaurea stoebe*, Cer arv: *Cerastium arvense*, Che alb: *Chenopodium album* agg., Con arv: *Convolvulus arvensis*, Con can: *Conyza canadensis*, Cre cap: *Crepis capillaris*, Cyn dac: *Cynodon dactylon*, Dip ten: *Diplotaxis tenuifolia*, Ech vul: *Echium vulgare*, Ely rep: *Elymus repens*, Ero cic: *Erodium cicutarium* agg., Eup cyp: *Euphorbia cyparissias*, Fes ovi: *Festuca ovina* agg. (i.e. *F. trachyphylla*, *F. duvalii*) Ger mol: *Geranium molle*, Koe mac: *Koeleria macrantha*, Lac ser: *Lactuca serriola*, Med fal: *Medicago falcata* x *varia*, Med min: *Medicago minima*, Myo ram: *Myosotis ramossisima*, Oen bie: *Oenothera biennis* s.l., Ono rep: *Ononis repens*, Pet pro: *Petrorhagia prolifera*, Phl phl: *Phleum phleoides*, Pla lan: *Plantago lanceolata*, Poa ang: *Poa angustifolia*, Pol avi: *Polygonum aviculare* agg., Pot arg: *Potentilla argentea*, Psy are: *Psyllium arenarium*, Rum ace: *Rumex acetosella*, Rum thy: *Rumex thyrsiflorus*, Sap off: *Saponaria officinalis*, Sed acr: *Sedum acre*, Sil con: *Silene conica*, Sil lat: *Silene latifolia* ssp. *alba*, Sil oti: *Silene otites*, Sil vul: *Silene vulgaris*, Sis alt: *Sisymbrium altissimum*, Tra dub: *Tragopogon dubius*, Tri arv: *Trifolium arvense*, Tri cam: *Trifolium campestre*, Ver phl: *Verbascum phlomoides*, Ver arv: *Veronica arvensis*, Vic lat: *Vicia lathyroides*, Vul myu: *Vulpia myuros*.

Phytomass of the ungrazed plots

By means of the mini-exclosures the phytomass of the ungrazed plots was assessed in order to provide a background for the following analyses. The effects of the variables "year", "plant functional type", "animal" and "vegetation type" on the phytomass were analysed by a mixed linear model. The results are shown in Table 5.1. The differences between the two vegetation types are not significant but there is a significant interaction "year*PFT", so Figure 5.2 gives the detailed results for both years and all three treatments.

effect	Num df	Den df	F Value	p
year	**1**	**12**	**33.57**	**<0.0001**
animal	**2**	**12**	**4.53**	**0.0199**
animal*year	**2**	**12**	**4.91**	**0.0277**
plant functional type (PFT)	**2**	**24**	**22.93**	**<0.0001**
year*PFT	**2**	**17**	**25.83**	**<0.0001**
animal*PFT	4	24	1.41	0.2592
animal*year*PFT	4	17	1.00	0.4358
vegetation type	1	12	1.22	0.2912
year*vegetation type	1	12	2.23	0.1614
animal*vegetation type	2	12	0.51	0.6127
animal*year*vegetation type	2	12	2.80	0.1006
vegetation type*PFT	2	24	3.23	0.0572
year*vegetation type*PFT	2	17	1.98	0.1683
animal*vegetation type*PFT	4	24	0.76	0.5605
animal*year*vegetation type*PFT	4	17	2.01	0.1393

Table 5.1. Result of the SAS mixed-linear-model analysis of the available phytomass at the ungrazed plots. Significant effects are shown in bold print. Num df: degrees of freedom Numerator; Den df: degrees of freedom Denominator; p: level of significance

Generally, phytomass was higher in 2004 than in 2003. This increase is expressed by a marked augmentation of herbs (x 6.6) and Fabaceae (x 2.9), while graminoids decreased (x 0.8). As a consequence, graminoids accounted for ca. 75 % of the phytomass in 2003 but only for 37 % in 2004. The factor "animal" is only weakly significant. As for this analysis the ungrazed plots were used, this is not a treatment effect but an a priori difference in the paddocks. On the paddocks with mixed grazing, the phytomass was somewhat higher in both years, but the composition was similar to that on the sheep and donkey paddocks. In the following only the percentages of grazed phytomass are considered, so that the slight differences among the paddocks do not interfere with these analyses.

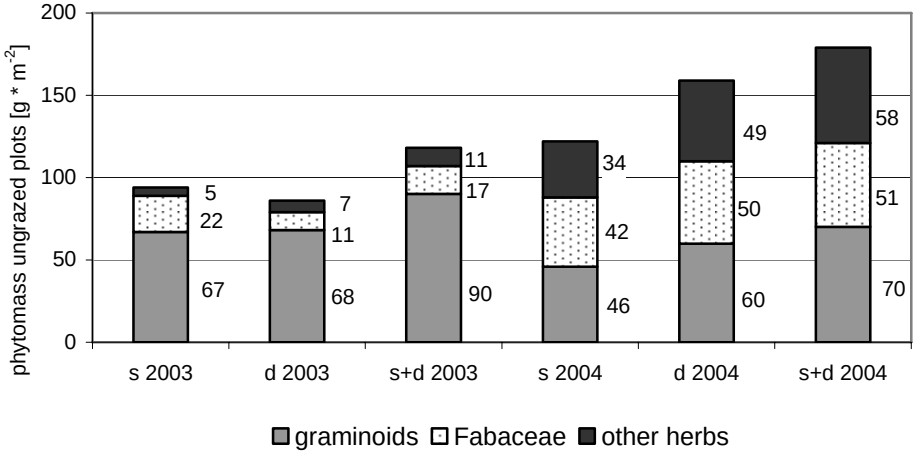

Figure 5.2. Phytomass composition of the ungrazed plots for the three grazing regimes in 2003 and 2004. s: sheep, d: donkeys, s+d: sheep followed by donkeys.

Phytomass extraction

Table 5.2 shows the result of the mixed-linear-model analysis of the relative phytomass extraction by the animals, not separated into different PFTs. The factor "animal" (experimental treatment) is significant. Whereas sheep and donkeys grazed on average approximately the same percentage of phytomass (see Table 5.3), grazing intensity was significantly and considerably higher in the case of the two-species treatment.

effect	Num df	Den df	F Value	p
year	1	12	0.13	0.7238
animal	**2**	**12**	**8.78**	**0.0045**
year*animal	2	12	2.15	0.1598
vegetation type	1	12	3.27	0.0958
year*vegetation type	1	12	0.00	0.9833
animal*vegetation type	**2**	**12**	**7.17**	**0.0089**
year*animal*vegetation type	2	12	0.06	0.9451

Table 5.2. Result of the SAS mixed-linear-model analysis of the percentage of grazed phytomass. Significant effects are shown in bold print. Num df: degrees of freedom Numerator; Den df: degrees of freedom Denominator; p: level of significance.

The significance of the interaction-term "animal*vegetation type" demonstrates that the grazing intensity also depends on the vegetation type: the *Festuca trachyphylla/duvalii*-community vegetation type is slightly grazed by sheep but significantly more intensively by the combination of sheep and donkeys. After Tukey-adjustment, the difference between sheep

and donkeys is slightly not significant (p = 0.06). Concerning the Armerio-Festucetum trachyphyllae vegetation type, donkeys grazed significantly less than the combination of sheep followed by donkeys, whereas the phytomass extraction of the sheep does not differ significantly from other treatments. Only in the case of sheep grazing could a significant difference between the percentage of grazed phytomass of both vegetation types be ascertained. Despite the marked difference of the phytomass of ungrazed plots between 2003 and 2004, the factor "year" does not influence the relative phytomass extraction (see Table 5.2).

effect		sheep	donkeys	sheep+donkeys
animal		51.9 (3.4) **a**	55.7 (3.4) **a**	71.1 (3.4) **b**
animal*veg	F	39.0 (4.9) **a,z**	61.2 (4.9) **ab,z**	67.7 (4.9) **b,z**
animal*veg	A	64.8 (4.9) **ab,y**	50.2 (4.9) **a,z**	74.4 (4.9) **b,z**

Table 5.3. Mean total phytomass extraction for the three grazing approaches. The standard errors resulting from the mixed-linear-model analysis are given in parentheses. a,b: average values within one row that are marked with different letters are significantly different; y,z: average values within one treatment that are marked with different letters are significantly different within the two vegetation types F: *Festuca trachyphylla/duvalii*-community, A: Armerio-Festucetum trachyphyllae.

Dietary preferences

To elucidate the dietary preferences of the animals on the level of PFTs "graminoids", "Fabaceae" and "other herbs", a mixed linear model was calculated with four independent factors. Table 5.4 shows the results.

effect	Num df	Den df	F Value	p
year	**1**	**12**	**7.98**	**0.0153**
animal	**2**	**12**	**13.36**	**0.0009**
year*animal	2	12	3.74	0.0545
plant functional type (PFT)	**2**	**24**	**16.01**	**<0.0001**
year*PFT	**2**	**17**	**8.10**	**0.0034**
animal*PFT	**4**	**24**	**7.13**	**0.0006**
animal*year*PFT	4	17	0.43	0.7876
vegetation type	**1**	**12**	**19.83**	**0.0008**
year*vegetation type	**1**	**12**	**4.77**	**0.0495**
animal*vegetation type	2	12	3.57	0.0609
animal*year*vegetation type	2	12	1.07	0.3725
vegetation type*PFT	**2**	**24**	**3.55**	**0.0447**
year*vegetation type*PFT	2	17	0.96	0.5605
animal*vegetation type*PFT	4	24	2.36	0.0823
animal*year*vegetation type*PFT	**4**	**17**	**4.24**	**0.0146**

Table 5.4. Result of the SAS mixed-linear-model analysis of the percentage of grazed phytomass differentiated into three plant functional types. Significant effects are shown in bold print. Num df: degrees of freedom Numerator; Den df: degrees of freedom Denominator; p: level of significance.

Since the highest-order interaction term “animal*year*vegetation type*PFT” is significant, the interpretation has to be differentiated. Figure 5.3 displays the percentage of grazed phytomass for each combination of factors.

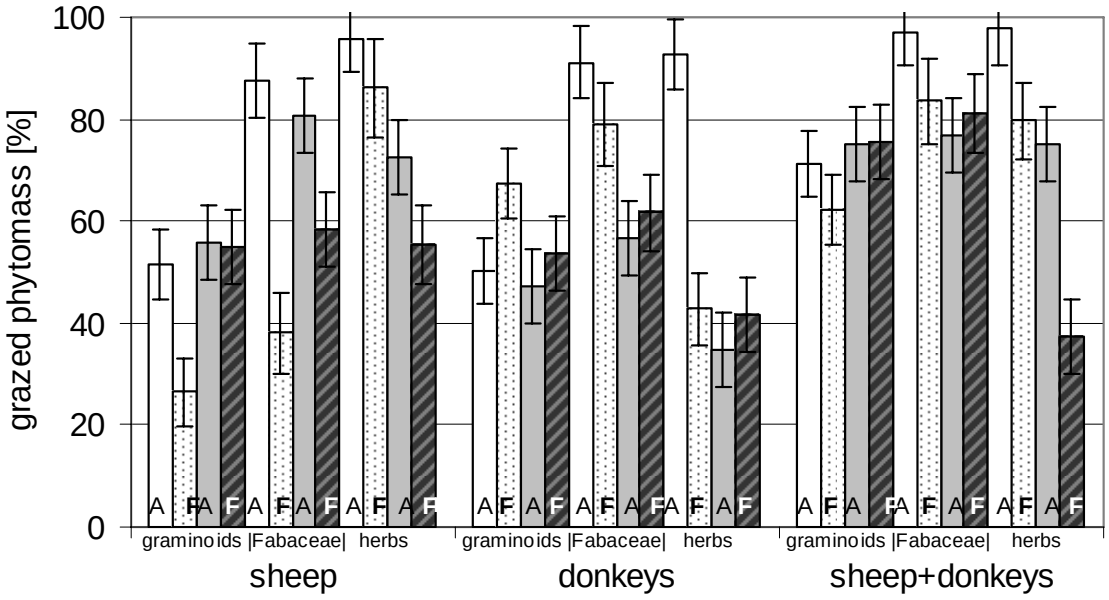

Figure 5.3. Mean percentages of grazed phytomass for every investigated category resulting from the mixed-linear-model analysis of the differentiated data set. Error: Standard error. A: Armerio-Festucetum trachyphyllae, F: *Festuca duvalii/trachyphylla*-dominated vegetation type, columns with white background: year 2003, columns with grey/black background: year 2004.

In Figure 5.4 mean values for the interaction “animal*PFT” have been calculated to show the most important results. Sheep strongly prefer “other herbs” (79 %) to graminoids (47 %) while Fabaceae occupy an intermediate position. Only in 2004 in the Armerio-Festucetum trachyphyllae was the grazing intensity on Fabaceae higher. In both years, more Fabaceae phytomass was consumed in the Armerio-Festucetum trachyphyllae vegetation type than in the *Festuca trachyphylla/duvalii*-community one. The low phytomass extraction of graminoids is very distinct in 2003 in the *Festuca trachyphylla/duvalii*-community.

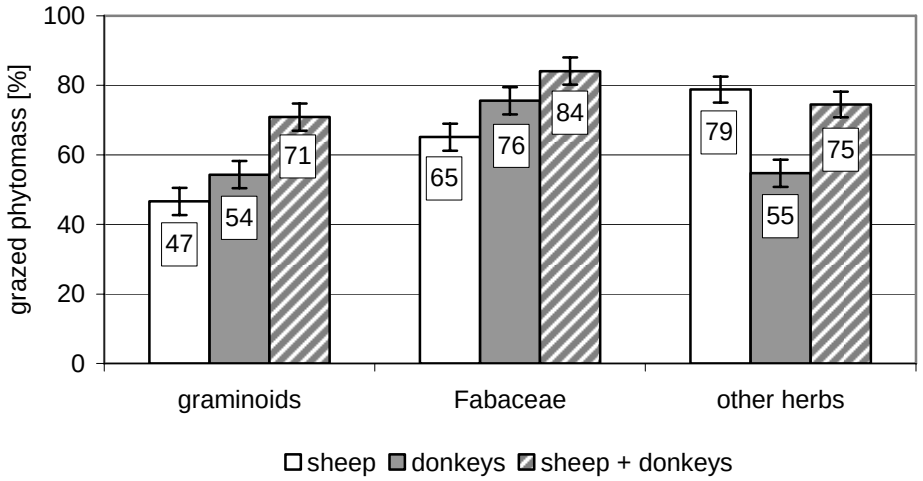

Figure 5.4. Mean percentages of grazed phytomass for the three treatments resulting from the mixed-linear-model analysis of the differentiated data set. Error: Standard error.

Donkeys have a preference for Fabaceae (76 %). Only in 2003 in the Armerio-Festucetum trachyphyllae vegetation type did they prefer “other herbs”. The difference in phytomass extraction between “other herbs” (55 %) and graminoids (54 %) is negligible and not significant.

The combined grazing resulted in a very high grazing impact on all PFTs and no significant differences between Fabaceae (84 %), “other herbs” and graminoids (71 %) can be detected. With the exception of a low grazing intensity in 2004 in the *Festuca trachyphylla/duvalli*-community, the combined grazing resulted in a very homogeneous and high extraction of phytomass.

Some informational background for the different grazing preferences is given in Table 5.5, where the dominant plant species in every category and the mean percentage of cover are shown. The most frequent species in the investigated PFTs are *Poa angustifolia* (graminoids), *Berteroa incana* (herbs) and *Medicago falcata* (Fabaceae). As also the phytomass of the ungrazed plots has shown, in 2003 cover of herbs was low, especially in the Armerio-Festucetum trachyphyllae vegetation type, and cover of Fabaceae species was also lower in 2003 than in 2004.

year	veg	PFT	sheep	donkeys	sheep + donkeys
2003	A	graminoids	Elymus repens (12 %)	Poa angustifolia (20 %)	Poa angustifolia (26 %)
2003	F	graminoids	Koeleria macrantha (15 %)	Koeleria macrantha (20 %)	Phleum phleoides (9 %)
2004	A	graminoids	Poa angustifolia (16 %)	Festuca trachyphylla (20 %)	Bromus hordeaceus (14 %)
2004	F	graminoids	Festuca duvalii/Koeleria macrantha (13 %)	Poa angustifolia (16 %)	Poa angustifolia (24 %)
2003	A	Fabaceae	Medicago falcata (17 %)	Medicago falcata (3 %)	Medicago falcata (8 %)
2003	F	Fabaceae	Ononis repens (14 %)	Medicago falcata (14 %)	Medicago falcata (7 %)
2004	A	Fabaceae	Medicago falcata (27 %)	Medicago falcata (23 %)	Medicago falcata (29 %)
2004	F	Fabaceae	Medicago falcata (19 %)	Trifolium arvense (17 %)	Medicago falcata (15 %)
2003	A	other herbs	Centaurea stoebe (2 %)	Cerastium arvense (1 %)	Saponaria officinalis (3 %)
2003	F	other herbs	Euphorbia cyparissias (3 %)	Armeria elongata (3 %)	Potentilla argentea (9 %)
2004	A	other herbs	Berteroa incana (14 %)	Berteroa incana (5 %)	Berteroa incana (5 %)
2004	F	other herbs	Euphorbia cyparissias (6 %)	Armeria elongata (6 %)	Verbascum phlomoides (8 %)

Table 5.5. Dominant plant species of the grazed mini-exclosure plots with average cover percentages in parentheses. PFT: plant functional type; veg: vegetation type; A: Armerio-Festucetum trachyphyllae; F: *Festuca trachyphylla/duvalii*-community.

Discussion

Grazing preferences on the species level

The investigation of the qualitative grazing preferences showed that only 54 % of the plant species were grazed by both animal species. In previous studies with cattle and horses as a model for ruminants and non-ruminants, a qualitative dietary overlap of about 70 % was found (Krysl et al. 1984, McInnis & Vavra 1987). Thus the comparatively small value for sheep and donkeys suggests that the present two animal species can complement each other very well. In the case of dominant graminoid species, sheep as well as donkeys feed on these often clonal species. The reduction of grasses by all three grazing regimes has been documented in a 3-year period (Süss et al. in prep.). On the other hand, the feeding on the endangered Red List species is problematic; hence care must be taken that grazing takes place after fruiting of these species, because in contrast to the dominant grass species they mostly reproduce generatively.

Phytomass extraction

Donkeys are supposed to need large phytomass intake because of their low nutrient extraction, and their dry matter intake is high compared to that of other herbivores (Aganga et al. 2000). As our study aims to compare different management methods, it is not possible to assess the need of one individual animal but to analyse the effects of the different grazing regimes on the vegetation. The results show that with one-species grazing (either sheep or donkey) the mean extraction of phytomass was about 50 - 60 %, but it depended on the vegetation type. With successive two-species treatment, a maximum phytomass extraction was obtained. A high phytomass extraction causes the regression of grass-encroachment and creates gaps for the less competitive plant species. The change of species composition by a reduction of dominant grass species with multi-species grazing (ruminants and non-ruminants) has also been observed by Loucougaray et al. (2004) in coastal ecosystems in France.

Dietary preferences

According to Hülber et al. (2005), "selective grazing occurs when the relative frequency of a food resource differs between the diet and the environment". In compliance with that definition, in our study sheep select for "other herbs" and Fabaceae, donkeys for Fabaceae. Usually livestock species prefer Fabaceae to other plant species, probably due to their higher protein contents (Stroh et al. 2002). Donkeys cannot store amino acids efficiently and therefore need a constant supply in their diet, which is provided by leguminous plant species (Aganga et al. 2000). Sheep are also known as selective grazers which prefer plant species with higher protein contents (Hafez 1962, Stroh et al. 2002). As is demonstrated in Figure 5.3, the sheep's preference of herbs to Fabaceae, as evidenced by the low phytomass extraction of Fabaceae by sheep in the *Festuca trachyphylla/duvalii*-community of the investigation area, can be explained by the high abundance of the Fabaceae species *Ononis repens* in that area; this plant is characterised by a high fibre content and thorns, so the animals prefer the leaves and reject the rough stem. The sheep's preference of leaves to stems has also been observed by O'Reagain (1993). This corresponds to the result that grasses - which usually have higher fibre contents - are least intensively grazed. Sheep, as a model species for ruminants, do not depend as heavily on roughage for their digestion as donkeys are known to do (Jeroch et al. 1999, Aganga et al. 2000).

Equids are considered to be "true grazers" that feed predominantly on grasses (Fahnestock & Detling 1999, Menard et al. 2002, Lamoot et al. 2005a). Although within the percentage analysis donkeys do not differentiate between herbs and grasses, Figure 5.2 demonstrates that graminoids form the main parts of their diet while herbs only contribute to a minor extent. Especially in the case of the Armerio-Festucetum trachyphyllae vegetation type in 2003, when relative phytomass extraction of herbs by donkeys was exceptionally high, this is due merely to an extremely low cover of herbal species, which is made evident by the very low mean cover (1 %) of the dominant herbal species *Cerastium arvense*.

The strong dependence on the year is probably mainly due to the different plant species composition in the two investigated years. Because of the dry conditions in 2003, therophytes - often herbs - were almost absent. This leads to the conclusion that dietary preferences are strongly dependent on the species composition, so that it is very important to investigate different years (Süss et al. submitted).

Successive two-species grazing

As the grazing regime is a successive one, no niche partitioning as described for other multi-species approaches (Menard et al. 2002) can be expected. Yet dietary overlap of 54 % is comparatively small. Hence, phytomass extraction is often highest in the case of successive ruminant and non-ruminant grazing, because the different preferences of the two animal species can complement each other. Another reason for the larger phytomass extraction in the case of the two-species treatment is the grazing of the donkeys' faeces-accumulation sites by sheep. In the case of equid grazing only, every year greater percentages of the paddock are used as faeces-accumulation sites with spreading ubiquitous nitrophytic plant species and ungrazed areas. This can be avoided by means of successive multi-species grazing (Jeroch et al. 1999, Loucougaray et al. 2004). So altogether, combined sheep and subsequent donkey grazing is the most effective method to achieve a high extraction of phytomass.

Conclusions for the management of threatened sand ecosystems

For purposes of nature protection, often a reduction of competitive grass species is necessary (Kooijman & van der Meulen 1996, Süss et al. 2004). The results demonstrate that a maximum extraction of grasses can be achieved by successive two-species grazing. Other investigations have shown that this leads to a reduction of grass cover throughout the years (Süss et al. in prep.). Donkey grazing is an appropriate tool for the management of sand ecosystems, but due to the occurrence of faeces-accumulation sites this grazing regime should be used rarely or in combination with grazing by other animals. Extensive sheep grazing with special breeds is a very effective method of ecosystem management but phytomass extraction is higher in the case of ruminant/non-ruminant grazing.

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Chapter 6:
Sheep versus donkey grazing or mixed treatment: results from a 4-year field experiment in Armerio-Festucetum trachyphyllae sand vegetation

Abstract

The abandonment of former land-use often leads to a decrease in community-specific plant species richness and to an increasing grass-encroachment. Extensive grazing can be an adequate management method, but the effects on the vegetation depend on the livestock species. We investigated two different subtypes of the Armerio-Festucetum trachyphyllae Hohenester 1960 (Armerion elongatae Poetsch 1962) in a dry and nutrient-poor inland sand ecosystem located in the Upper Rhine Valley (Germany). The two subtypes reflect gradients towards progressively more dense grassland. We chose local sheep breeds and donkeys as grazing animals which are adapted to these conditions. In four vegetation periods (2002 - 2005), the influences of three grazing regimes on the floristic structure of the plant communities were investigated: sheep grazing (s), donkey grazing (d) and the successive combination of sheep and donkeys (s+d).

For both vegetation subtypes, every treatment was replicated thrice on paddocks 700 m² in area. The vegetation was recorded by 1200 relevés (2002-2005: s, d) and by further 429 relevés (2003-2005: s+d). Additionally, we obtained data on species composition, nitrogen input and phytomass at special donkey-generated microsites.

The factors “year” and “vegetational subtype” had a strong influence on vegetation parameters. Species number, especially therophytes, was higher, cover of graminoids was lower for donkey grazing than for sheep grazing. Donkeys create a vegetation pattern with a variety of microsites. Nitrogen input at donkeys’ faeces sites was 223 kg N * ha^{-1}, 4 % of the paddock area was affected. The phytomass at faeces sites was lower after 15 weeks and identical after 45 weeks in relation to controls.

Sheep grazing is an adequate management method for intact sand ecosystems but for more ruderalised plots a combination of both species can become an important management tool.

Introduction

In many countries of Central Europe the abandonment of former land-use as well as an increasing nitrogen deposition lead to a progressive decrease of plant species richness and to an increase of highly competitive, often clonal grass species (ten Harkel et al. 1995, de Bonte et al. 1999, Süss et al. 2004). During recent years, extensive grazing has turned out to be an important tool of fallow grassland management to restore ecosystems with formerly high phytodiversity (e.g. Kooijman & van der Meulen 1996, Hellström et al. 2003, Schwabe et al. 2004). As well as reducing dominant grass species, grazing produces gaps — an important effect because regeneration niches sensu Grubb (1977) for the germination of poorly competitive plant species are thus created (Bullock et al. 1994, Olff & Ritchie 1998, Provoost et al. 2002, Fynn et al. 2004).

In this study we investigated a dry inland sand ecosystem; a threatened habitat of numerous endangered site-specific plant species. In the long run, the Armerio-Festucetum trachyphyllae Hohenester 1960, which was used as a model system, is dependent on special management to stop grass-encroachment. The association belongs to the Armerion elongatae Poetsch 1962, which some authors (e.g. Oberdorfer 1993) regard as an alliance belonging to the Festuco-Brometea, whereas others (e.g. Berg et al. 2004) consider it an alliance belonging to the Koelerio-Corynephoretea; both views reflect the transitional position of the alliance.

Great care must be taken to choose suitable livestock species, depending on the ecosystem. In the case of such a low-productivity ecosystem, grazing animals have to be adapted to nutrient-poor conditions. Often sheep, especially local sheep breeds, are used for the management of these open habitats. But also donkeys, due to their origin in a hot and semi-arid environment, are well adapted to dry and nutrient-poor conditions (Pearson et al. 2001). The opportunity to use donkeys for the management of these ecosystems was recently also pointed out by Lamoot et al. (2005), who found out that donkeys are sufficiently nourished by the scarce vegetation of coastal sand ecosystems. Although both animal species can cope with these conditions, the grazing impact can be different due to the specific behaviours and requirements of sheep (ruminants) and donkeys as representatives of equids (non-ruminants). Hence, identical effects due to a general grazing influence and divergent effects due to the specific behaviours and requirements of different livestock species are expected. To clarify the different impacts of the two livestock species, we expected that a large number of plots would have to be tested. Since many studies have already proved the effectiveness of sheep grazing for our system (e.g. Stroh et al. 2002, Schwabe & Kratochwil 2004, Schwabe et al. 2004), in the present study the main emphasis was placed on comparing it with two other

grazing regimes for the management of dry sand ecosystems (sheep grazing vs. donkey grazing and sheep followed by donkey grazing).

Donkeys can have a strong impact on the structure of the paddocks by the creation of microsites. As is typical of equids, donkeys produce wallows for sand-bathing by rolling (Bogner & Grauvogl 1984). They also tend to scratch the ground so as to dig out the roots of palatable plant species (Canacoo & Avornyo 1998). Sheep in the investigated plant communities produce smaller and more homogeneously distributed gaps by trampling, and it is only if they are kept on larger paddocks for a longer period that linear paths of bare ground can develop (Schwabe et al. 2004).

Concerning the diet preferences, sheep graze more intensively on herbs while donkeys prefer Fabaceae and graminoids in the investigated ecosystem (Süss et al. submitted). Therefore we supposed that these two animal species would complement each other well (Stroh et al. 2002). Also with regard to their eliminative behaviour, the two species are substantially different. Whereas sheep tend to eliminate where they graze and produce an accumulation of pellets (Bogner & Grauvogl 1984) that are soon spread by wind and rain, donkeys establish latrine areas for the excretion of faeces as well as urine, and seek these out for the purpose of elimination (Bogner & Grauvogl 1984). As a consequence, in the case of sheep grazing with large herds, the paddocks are rather homogeneously spread with faeces pellets whereas the distribution of donkey faeces is more patchy, with large unaffected areas and small highly concentrated faeces sites. This has consequences for the horizontal distribution of nutrients, especially nitrogen, and thus can influence plant species composition and grazing intensity.
As the animals avoid grazing near their own faeces sites as a strategy for defence against parasites, a mosaic grazing pattern specific for equids is observed in the case of donkey grazing (Bogner & Grauvogl 1984, Loucougaray et al. 2004). Ungrazed spots with a more ruderal plant species composition can occur. This may be compensated by a combination of both animal species in a successive multi-species approach (Jeroch et al. 1999).
So in addition to the investigation of single sheep or donkey grazing, we also investigated a multi-species approach with sheep and afterwards donkey grazing, because donkeys are still able to find food where sheep no longer graze and “can feed on a variety of stuff” (Aganga et al. 2000).
In general, the combination of ruminants and non-ruminants in a multi-species grazing approach has recently been discussed as a measure of ecosystem management following

traditional land-use (Menard et al. 2002, Loucougaray et al. 2004). The successive combination of different herbivores has also been proposed by Coffey (2001).
Regarding the agroeconomical context, sheep in our investigation area are integrated in a system of direct marketing of high-quality meat from nature protection areas (Mährlein, 2004), while donkeys are mainly used for breeding purposes and to assist public relations of a nature protection association.

In this study, we investigated two vegetational subtypes of our model system throughout 3 years of treatment with sheep, donkeys and the successive combination of both to analyse the effects of the three grazing regimes on the vegetation. The analyses of the vegetation of special sites connected with donkey grazing (e.g., wallows or faeces accumulation sites) and of the nitrogen input and the degradation of nitrogen at donkeys' faeces accumulation sites are used as information for final interpretation. To clarify the different effects of the investigated management methods we focus on the following questions:

1. How does the vegetation respond to sheep or donkey grazing, and to successive two-species grazing? What kind of plant species or plant functional types benefit or suffer from which grazing regime?
2. How intensive is the creation of gaps in case of the three treatments?
3. What is the role of special sites (e.g. wallows, faeces accumulation sites) in case of donkey grazing; is the plant species composition different from that of the control plots?
4. How strong is the nitrogen input at the donkeys' faeces accumulation sites and what is the time course of nitrogen content over a certain period?
5. As a consequence of 1- 4: which treatment is best suited as a management method for the investigated plant communities as models for low-productivity systems?

Materials and methods

Study area

The investigation took place during the years 2002 to 2005 in the northern Upper Rhine Valley (Germany) about 30 km south of Frankfurt/Main (Hesse) near Darmstadt. A 71-ha nature reserve ("Ehemaliger August-Euler-Flugplatz") served as a model area for grazed inland sand ecosystems. The substrate is drifted sand which had been blown-out from calcareous Rhine deposits during late glacial and post-glacial periods. The investigation site is covered by the Armerio-Festucetum trachyphyllae vegetation complex, which is characteristic

for more consolidated conditions and partial decalcification in the upper soil (lime content is set between 0.23 and 8.89 %). Since 1999, the whole area has been grazed by sheep as a management tool against grass-encroachment and succession (Schwabe et al. 2002). Donkey grazing started in 2002 and successive two-species grazing in 2003. These paddocks were formerly sheep-grazed. Additionally, there was a strong influence of rabbits in all paddocks, reflecting a natural biotic factor in sand ecosystems. Results of rabbit exclosures which have now been running for ten years show that there are structural effects but no pronounced effects concerning the change of floristic structure.

The climate of the investigation area is characterised by a considerable annual fluctuation with a mean annual temperature of 10.8 °C, 1686 hours of sunshine and a precipitation rate of around 600 mm per year (data for the years 1991-2005 from Frankfurt/Main airport; Internet). The investigated years 2002, 2004 and 2005 more or less fit within the long-term average with a slightly higher precipitation rate in 2002 (777 mm) while 2003 was an extraordinary year with a higher temperature (11.4 °C), a longer duration of sunshine (2138 h) and an extremely low precipitation rate (379 mm) compared to “normal” years. So in the following, 2003 is regarded as a model year for extreme climatic conditions as discussed for example by Ciais et al. (2005) (also Schär et al. 2004, Meehl & Tebaldi, 2004) while 2004 has the character of a “response” year and 2002 and 2005 represent rather normal climatic conditions for the investigated area.

Experimental design

The investigated area was stratified according to the two investigated vegetational subtypes of the Armerio-Festucetum trachyphyllae, the *Festuca duvalii*-subtype (F), characterising more open and base-rich sites and Armerio-Festucetum trachyphyllae typicum (A). The two subtypes reflect a gradient towards progressively more dense sward, followed by top-soil acidification. In each of them 9 paddocks of around 700 m² were chosen. The three treatments (sheep grazing, donkey grazing, sheep followed by donkey grazing) were assigned to three paddocks each. Thus, the investigation was replicated thrice. Every paddock consists of 25 (sometimes 24) plots, each 25 m² in size. Every year in June, before grazing took place, at each 25 m² plot the vegetation was recorded on a percentage scale. Nomenclature of the phanerogams follows Wisskirchen & Haeupler (1998), that of the bryophytes, Koperski et al. (2000) and that of the lichens, Scholz (2000). *Medicago falcata* and the hybrid *M. sativa* x *falcata* (= *M.* x *varia*) were pooled. In total, 443 plots were analysed, i.e. 1629 relevés

throughout the whole investigation period. For the calculation of the mean cover values of each paddock, each absence of a species at one plot was counted as "0 %" only if the species was present at least once within the four years at the plot concerned and is thus a representative of the species pool.

Grazing regime

The paddocks were grazed during summer by about 500 sheep, and/or by 2-3 adult donkeys and one foal. The sheep grazing regime was a dynamic one with intensive short-term grazing of small paddocks (about 1 ha) once a year for 1-2 days where the above-mentioned paddocks were integrated. The donkeys grazed the approximately 700 m² paddocks for about 3-5 days, depending on the amount of phytomass. Both animal species, sheep as well as donkeys, grazed the paddocks as long as an adequate food supply could be guaranteed. In the case of the successive sheep and donkey grazing, at first the paddocks were grazed by sheep in the same manner as described above and a few days later the grazing-leftover was grazed by the donkeys for about 1-2 days again.

Percentage of bare ground and cover of seedlings

The percentage of bare ground for each 25-m² plot was estimated every year in combination with the yearly vegetation relevés in June before grazing. To test for differences in the creation of gaps by the grazing animals, the percentage of bare ground was additionally estimated about 4 weeks after grazing in September 2003 (only at the Armerio-Festucetum trachyphyllae typicum). At all plots it was again recorded at the end of October 2003. In 2004, the percentage of bare ground was estimated immediately after grazing of each plot as well as at the end of October. Together with the October estimation in 2003 and 2004 - the germination time of the late autumn seedlings - also the cover of seedlings per plot was estimated.

Investigation of special sites resulting from donkey grazing

The donkeys created four kinds of disturbance sites: nutrient-affected plots, i.e. faeces and urine accumulation sites, on the one hand and gaps of bare ground, i.e. wallows and scratch sites, on the other hand. These microsites found in the first grazing period 2002 were marked and recorded as well as neighbouring control sites of the same size (always about 1 m², referring to the natural dimensions). The vegetation of these plots was recorded in 2003 and 2004 according to a percentage scale.

Nitrogen input and vegetation parameters of faeces accumulation sites

The cover percentage of donkey faeces was estimated immediately after grazing in 2004. To analyse the nitrogen input and the decrease of nitrogen along a time-gradient, dung plots measuring 20 cm x 20 cm were investigated, by collecting all faeces on each plot. The time-span between the samples was doubled: immediately after grazing of each plot in summer 2004 (t_0), after 1 week (t_1), 3 weeks (t_2), 7 weeks (t_3), 15 weeks (t_4) and after 45 weeks in June 2005 (t_5). Two replicates for each grazed paddock and for every point in time were taken. Plots were fenced against rabbits (mesh width 2.5 cm) and faeces was fixed with a net having 6-mm mesh width. After sampling, the faeces was dried for 48 h at 70 °C, weighed and ground to a powder. By means of a N-analyzer (Carlo Erba 1400), total nitrogen content was determined. Accuracy was ascertained by certified material (hay powder standard provided by the Community Bureau of References, 99.7 % of certified value, n = 6).

The vegetation of the faeces accumulation sites as well as of the urine sites was analysed in November 2004 (t_4) and in June 2005 (t_5). Two faeces sites, one urine site and two controls for each paddock were sampled in both years. The plots were 40 cm x 40 cm in size and fenced in the same manner as described above. The vegetation was recorded on a percentage scale and afterwards clipped to the level of the faeces, i.e. to the cryptogam layer, dried for 48 h at 70 °C and weighed.

Statistical analyses

The floristic structure of the plots was analysed by means of detrended correspondence analysis (DCA), calculated with PC Ord 4.0. The analysis was run with downweighting and rescaling of the axes, the number of segments was 26. For the DCA as well as for all other analyses of these plots, the arithmetic mean of the data of the 25 plots forming one paddock was used. The mean cover percentages were used without transformation.

To analyse the effects of the independent variables “animal”, “year” and “vegetation type” on the vegetation parameters, mixed linear models were calculated (SAS 8.02, Proc Mixed), which are especially suited for analysing repeated measures data (Littell et al. 1998), because they allow comparison of the goodness of fit of several covariance structures. We tested autoregressive (1), heterogeneous autoregressive (1), autoregressive moving averages (1,1), unstructured, compound symmetry and Huynh-Feldt and chose the one with the best Akaike (AIC) values for the final calculations. Post hoc multiple comparisons were Tukey-adjusted.

The status quo years 2002 for the partitioning of sheep- and donkey grazing, and 2003 for successive two-species grazing were analysed separately to test for initial differences between the plots. Afterwards the remaining 3 and 2 treatment years, respectively, were analysed.

Results

Influence of the year

Throughout all analyses, the factor "year" was mainly the most significant parameter. In most cases, the extreme year 2003 was different from the remaining investigated years and was for example characterised by a reduced number of species, especially therophytes (see Figure 6.1). As a consequence, for some variables – as described in the following – an extraordinary increase in the year 2004 was observed. This was consistent for all grazing regimes and was also observed in case of neighbouring ungrazed exclosures (Schwabe et al. unpublished data). But apart from general trends that were consistent throughout all three investigated grazing regimes, effects were different for the three treatments.

Number of plant species

As shown in Figure 6.1, the mean number of species per 25-m² plot in the *Festuca duvalii*-subtype was significantly higher in the case of donkey grazing than with sheep grazing in 2003 ($p = 0.011$) as well as in 2005 ($p = 0.030$). In 2003, this was mainly due to a significantly higher number of therophytes at the donkey-grazed areas ($p = 0.004$) than at the sheep grazed ones. In 2005, after two years of combined sheep- and donkey-grazing, the number of therophytes at the two-species treatment plots ($p = 0.019$) as well as that of the donkey-grazed paddocks ($p = 0.024$) was significantly higher than that of the sheep-grazed paddocks. There was no significant initial difference between sheep- and subsequently donkey-grazed sites concerning the total number of plant species as well as the number of therophytes in 2002 as well as between sheep-grazed and successive sheep- and donkey-grazed plots in 2003. Regarding the number of hemicryptophytes, other life forms and cryptogams, no significant differences between the three treatments were observed within the same year and the same vegetation type.

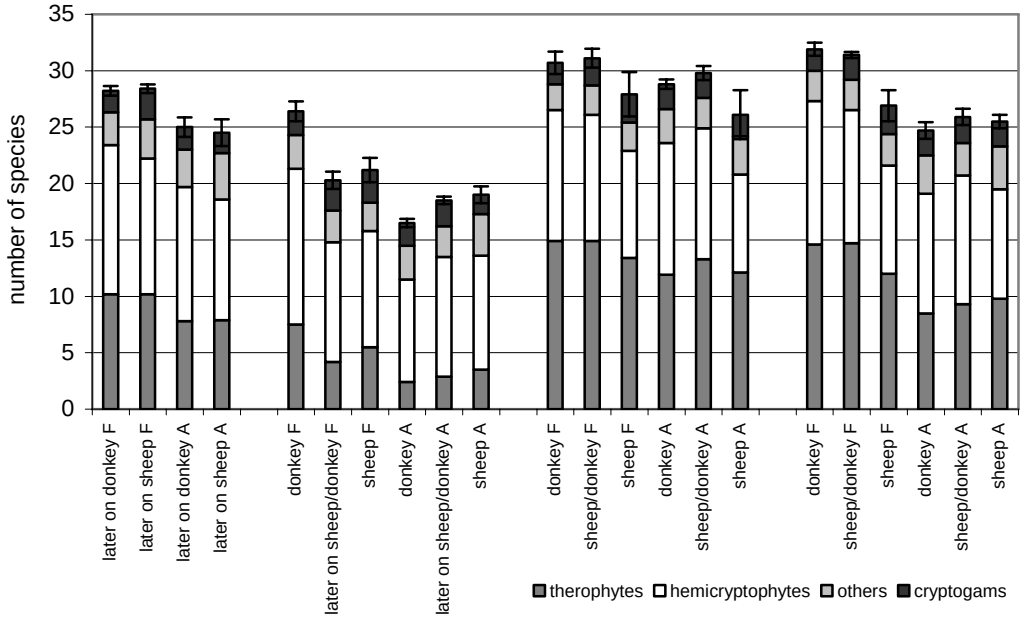

Figure 6.1. Species number for the investigated years, treatments and vegetation types, separated into "therophytes", "hemicryptophytes", "cryptogams" and "other life forms". F: *Festuca duvalii*-subtype, A: Armerio-Festucetum trachyphyllae typicum. The standard error of the total species number is given.

Cover of different vegetation layers

Concerning the percentage cover of different vegetation layers and litter, the general trend of all grazing regimes was a decrease of graminoids and litter whereas the cover of herbs increased (see Figure 6.2). There are some significant differences between the treatments. Since the two-species treatment is not significantly different from the rest in the "effect" years, only the results of the mixed linear model analyses for the effect years 2003 – 2005 for sheep and for donkeys are shown in Table 6.1. Except for the litter layer of the *Festuca duvalii*-subtype - where the cover of the subsequently donkey-grazed paddocks was significantly ($p = 0.004$) higher than that of the sheep-grazed ones – no initial differences in the status quo year 2002 were detected. The difference was negated in the following years due to a strong decrease of the litter layer at the donkey-grazed paddocks.

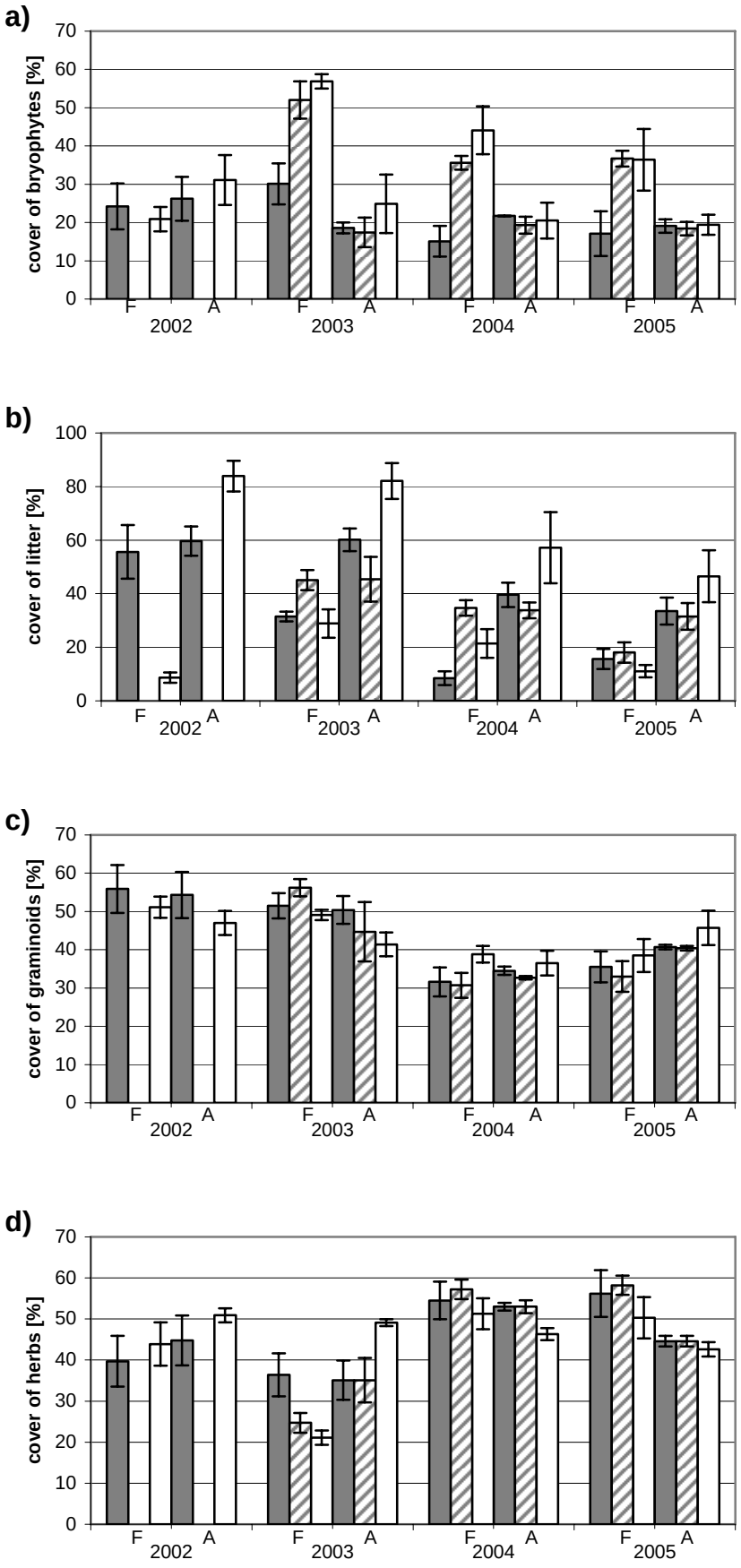

Figure 6.2. Cover of a) bryophytes, b) litter, c) graminoids and d) herbs for donkey grazing (grey), mixed treatment (grey and white) and sheep grazing (white). F: *Festuca duvalii*-subtype, A: Armerio-Festucetum trachyphyllae typicum. Error: standard error.

graminoids	Num df	Den df	F-Value	p
Veg	1	7.87	0.07	0.8025
Animal	1	7.87	0.12	0.7382
Veg*Animal	1	7.87	0.34	0.5748
Year	2	15.20	49.74	<0.0001
Veg*Year	2	15.20	4.96	0.0220
Animal*Year	2	15.20	7.91	0.0044
Veg*Animal*Year	2	15.20	1.04	0.3761

herbs	Num df	Den df	F-Value	p
Veg	1	7.84	0.29	0.6061
Animal	1	7.84	0.19	0.6740
Veg*Animal	1	7.84	1.02	0.3428
Year	2	11.00	35.71	<0.0001
Veg*Year	2	11.00	11.09	0.0023
Animal*Year	2	11.00	5.16	0.0264
Veg*Animal*Year	2	11.00	6.32	0.0149

bryophytes	Num df	Den df	F-Value	p
Veg	1	8.02	8.59	0.0189
Animal	1	8.02	9.79	0.0140
Veg*Animal	1	8.02	7.36	0.0265
Year	2	15.40	9.52	0.0020
Veg*Year	2	15.40	6.77	0.0078
Animal*Year	2	15.40	1.01	0.3886
Veg*Animal*Year	2	15.40	1.80	0.1980

litter	Num df	Den df	F-Value	p
Veg	1	9.70	44.47	<0.0001
Animal	1	9.70	5.63	0.0398
Veg*Animal	1	9.70	1.64	0.2306
Year	2	16.70	23.52	<0.0001
Veg*Year	2	16.70	2.58	0.2058
Animal*Year	2	16.70	4.41	0.0290
Veg*Animal*Year	2	16.70	4.18	0.0337

Table 6.1. Results from the mixed linear model analyses of the cover of graminoids, herbs, bryophytes and litter. Veg: vegetational subtype, Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Regarding the effect years, for the litter layer as well as for the cover of herbs, the highest-order interaction term “Vegetation type*Animal*Year” is significant, but analysis of the detailed results shows that this is only due to differences across different years and different vegetation types and is therefore not relevant for our investigation. Donkey grazing and sheep grazing show significant differences in case of the graminoid layer. The interaction term “Animal*Year” is significant. The reduction of graminoid cover in the “response” year 2004 is consistent for all treatments but only for donkey grazing the graminoid cover is significantly reduced in 2005 in relation to 2003 ($p = 0.001$) while for sheep grazing there is no significant difference between these years and only the “response” year 2004 shows a decrease in graminoid cover ($p = 0.010$). In case of the bryophytes, the difference depends not

on the year but on the vegetation type, the cover of bryophytes of the sheep-grazed paddocks at the *Festuca duvalii*-subtype being larger than that of the donkey-grazed plots ($p = 0.014$). As an initial difference, the successively two-species-grazed paddocks of the Armerio-Festucetum trachyphyllae typicum in 2003 were characterised by a lower cover of litter than the sheep-grazed paddocks. Due to a decrease of litter at the only sheep-grazed paddocks from 2003 to 2004 this difference was negated in the following years.

Influence on certain plant species (Table 6.2)

The degree of presence as well as the mean cover values of the species are shown in Table 6.2 for each year, grazing regime and vegetation type. Each plant species present in at least one third of the relevés was analysed for differences between the three grazing regimes. Plant species that increased in their degree of presence with donkey grazing were *Potentilla argentea* agg., *Carduus nutans* and *Arabidopsis thaliana* while *Petrorhagia prolifera* and again *Potentilla argentea* agg. had higher cover values. *Agrostis capillaris* decreased in its degree of presence with donkey grazing and *Berteroa incana* and *Erodium cicutarium* in their mean cover values. *Bromus hordeaceus* increased in its degree of presence with donkey grazing and in its cover values with sheep grazing while *Centaurea stoebe* was reduced by both grazing regimes but to a stronger degree with sheep grazing. The plant species *Trifolium arvense* was increased with donkey grazing and decreased with sheep grazing while the opposite effect was observed for *Medicago falcata / M.* x *varia*. Very weakly significant effects were also detected for *Crepis capillaris* and *Conyza canadensis*, but these species were probably significant by accident due to the high number of relevés. The results of the mixed linear model analyses are shown in Table 6.3 for every significant plant species and the highest significant interaction term.

Table 2. Presence table with mean cover values grouped for each grazing regime, vegetation type and year. D: donkeys, S: sheep, S+D: sheep followed by donkey grazing; d.p.: degree of presence; bt: before treatment, F: *Festuca duvalii*-subtype, A: Armerio-Festucetum trachyphyllae typicum; +: mean cover < 0.5 %; dot: species not present; FB: Festuco-Brometea, Ko: Koelerio-Corynephoretea, S: Stellarietea mediae, Ag: Agropyretea, Ar: Artemisietea, M: Molinio-Arrhenatheretea, O: Other species; Life form: C: chamaephyte, G: geophyte, H: hemicryptophyte, P: phanerophyte, T: therophyte; PFT: plant functional type: F: Fabaceae, G: graminoids, H: herbs; B: Bryophytes, L: Lichens.

phytosoc. group	Life form	PFT		d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%	d.p.	%
			Year	2002		2003		2004		2005		2002		2003		2004		2005		2002		2003		2004		2005		2002		2003		2004		2005		2003		2004		2005	
			Animal	bt		D		D		D		bt		D		D		D		bt		S		S		S		bt		S		S		S		bt		S+D		S+D	
			Vegetation type	F		F		F		F		A		A		A		A		F		F		F		F		A		A		A		F		F		F	
			Number of relevés	75		75		75		75		75		75		75		75		75		75		75		75		75		75		75		70		70		70	
			Mean species number	28,6		26,3		30,6		32,0		25,0		16,3		28,8		25,3		28,4		21,1		27,9		27,2		24,5		18,9		26,2		25,5		20,3		31,1		31,4	
			Span species number	20-36		20-36		22-39		21-39		19-34		13-21		22-40		20-30		17-36		15-30		20-36		20-37		18-32		13-24		19-34		19-32		12-28		23-37		25-36	
			Donkeys: significant effects increase																																				
Ko	H	H	Potentilla argentea agg.	71	1	88	2	77	1	87	3	84	2	92	2	89	2	97	6	83	3	76	2	64	1	68	2	17	+	35	1	25	+	33	1	77	2	66	1	65	2	85	2	67	1	86	3
Ar	H	H	Carduus nutans	17	+	37	+	32	+	35	1	31	+	48	+	88	1	87	2	17	1	16	+	11	+	7	+	12	+	17	+	39	+	39	1	26	+	51	+	47	1	58	1	83	1	78	2
S	T	H	Arabidopsis thaliana	9	+	1	+	87	1	32	+	.	.	.	.	.	.	.	.	.	.	.	.	9	+	3	+	1	+	3	+	3	+	3	+	1	+	39	1	22	+	.	.	3	+	.	.
Ko	T	H	Arenaria serpyllifolia agg.	81	1	65	1	96	3	89	1	39	+	.	.	88	2	91	1	99	1	24	+	100	2	100	4	36	+	.	.	88	+	97	2	12	+	93	2	96	1	.	.	97	1	92	2
Ko	T	H	Petrorhagia prolifera	47	1	15	+	32	+	71	+	31	1	.	.	7	+	.	.	13	1	.	.	3	+	11	+	35	1	4	+	5	+	11	+	.	.	39	+	52	+	.	.	10	+	4	+
			decrease																																				
O	H	G	Agrostis capillaris	48	2	69	2	9	+	5	+	23	1	12	+	25	+	20	1	5	1	5	1	.	.	1	+	8	+	23	+	4	+	9	+	2	+	.	.	9	+	13	1	7	+	9	1
Ar	T	H	Berteroa incana	51	1	43	1	44	1	27	1	83	2	61	1	89	3	53	+	19	1	9	+	7	+	7	+	97	4	97	3	99	5	97	2	23	+	39	2	28	1	75	1	85	4	52	1
Ko	T	H	Erodium cicutarium agg.	76	1	85	1	100	5	55	1	92	1	36	+	85	2	71	2	95	1	97	1	100	8	75	2	87	1	27	+	97	2	81	1	74	1	94	6	63	1	58	1	97	3	86	2
			Sheep, donkeys: significant effects																																				
S	T	G	Bromus hordeaceus	17	+	63	2	72	1	72	3	92	3	95	5	92	3	97	4	3	+	5	+	16	+	15	+	93	4	99	5	100	10	100	15	6	+	40	+	51	1	89	3	100	6	99	7
FB	H	H	Centaurea stoebe	93	3	69	1	83	1	93	3	96	4	55	+	83	+	57	+	51	2	23	+	17	+	9	+	100	6	93	2	76	+	68	1	17	+	39	+	39	2	68	1	71	1	52	1
			Sheep, donkeys: divergent effects																																				
Ko	T	F	Trifolium arvense	88	1	1	+	56	+	95	3	19	+	.	.	33	+	1	+	55	2	1	+	31	+	29	+	20	1	.	.	31	+	7	+	.	.	46	1	63	2	.	.	32	+	6	+
FB	H	F	Medicago falcata / M. x varia	89	6	89	7	81	4	88	4	96	5	99	7	96	10	96	6	67	7	75	6	72	4	69	5	96	8	99	16	99	14	100	14	80	3	80	5	79	4	100	13	96	13	100	13
			Ch, d Armerio-Festucetum trach.																																				
Ko	H	H	Armeria maritima ssp. elongata	84	4	87	3	65	2	76	3	96	3	93	2	83	2	85	2	60	2	35	1	39	1	37	1	93	2	96	3	64	1	81	2	38	1	61	2	62	3	93	3	77	2	89	3
O	H	G	Festuca trachyphylla	85	3	97	3	68	1	56	1	100	5	100	4	97	3	91	1	97	4	97	4	95	3	91	2	97	5	97	4	79	2	77	1	88	3	79	1	77	2	79	3	85	2	90	2
Ag	C	H	Cerastium arvense	45	2	67	3	56	2	56	2	80	5	79	3	65	2	88	3	40	2	45	2	49	2	43	2	85	5	81	4	76	2	91	3	41	3	42	2	36	2	81	4	72	2	82	4
FB	H	G	Koeleria macrantha	99	10	100	11	100	7	100	10	87	5	95	5	100	6	99	8	100	9	100	9	100	8	99	8	100	6	99	5	100	5	100	9	100	7	100	9	95	9	100	6	100	6	100	10
M	H	H	Achillea millefolium	45	1	59	1	37	+	41	+	68	1	31	+	48	+	9	+	40	2	40	1	23	+	9	+	87	1	65	1	19	+	4	+	60	1	27	+	27	+	38	+	25	+	7	+
Ko	H	H	Rumex acetosella	63	1	51	1	63	1	85	4	.	.	3	+	41	1	43	2	67	2	24	+	55	1	79	2	8	+	8	+	21	+	33	1	32	+	69	1	73	4	7	+	34	4	33	4
Ko	HT	F	Vicia lathyroides	48	+	9	+	88	+	88	+	67	1	.	.	83	+	60	+	39	+	12	+	95	+	72	+	91	1	1	+	91	+	83	+	32	+	82	+	73	+	.	.	84	+	81	+
FB	H	G	Phleum phleoides	24	1	32	2	8	+	24	1	24	2	7	1	.	.	16	1	11	1	5	+	.	.	3	+	23	1	16	1	4	+	7	+	12	2	9	+	13	+	1	1	.	.	3	+
Ko	T	H	Myosotis ramosissima	21	+	.	.	76	2	67	+	15	+	.	.	41	+	57	+	3	+	.	.	52	+	52	2	16	+	.	.	45	+	53	+	1	+	34	+	62	+	.	.	52	+	47	+
			d Festuca duvalii subcommunity																																				
Ko	H	G	Festuca duvalii	9	3	11	1	7	1	8	1	1	5	.	.	.	.	.	.	77	8	76	10	80	6	71	5	.	.	.	.	3	+	.	.	29	2	31	2	63	2	.	.	.	.	.	.
Ko	H	H	Helichrysum arenarium	8	2	9	1	5	+	3	+	.	.	.	.	.	.	.	.	11	1	7	+	1	+	1	+	1	1	.	.	.	.	.	.	4	1	1	+	.	.	.	.	.	.	.	.
Ko	T	H	Myosotis stricta	3	+	.	.	31	+	17	+	.	.	.	.	.	.	.	.	4	+	.	.	33	+	3	+	.	.	.	.	.	.	.	.	.	.	27	+	29	+	.	.	.	.	3	+
Ko	T	H	Veronica praecox	5	+	.	.	.	.	11	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	1	.	.	.	.	.	.	.	.	.	.	1	+	19	+	.	.	.	.	.	.
Ko	H	G	Poa bulbosa	.	.	.	.	11	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	3	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	.	.	.
Ko	T	H	Erophila verna	.	.	.	.	3	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13	+	3	+	.	.	.	.	.	.	.	.	.	.	4	+	.	.	.	.	.	.	.	.
			Koelerio-Coryneph. species as gap pioneers																																				
Ko	H	H	Echium vulgare	79	2	67	1	81	1	55	2	19	+	9	+	21	+	17	+	80	2	85	2	80	1	57	1	7	+	4	+	7	+	12	+	62	1	74	1	57	1	16	+	24	+	23	+
Ko	C	H	Sedum acre	69	1	72	+	32	+	77	1	19	+	5	+	33	+	61	1	79	1	15	+	13	+	64	1	47	1	16	+	45	+	67	1	35	+	39	+	75	+	16	+	38	+	56	1
Ko	T	H	Silene conica	33	+	21	+	67	1	67	1	27	+	1	+	43	+	4	+	65	1	19	+	69	1	59	+	24	+	1	+	37	+	12	+	7	+	74	1	60	1	.	.	51	+	12	+
Ko	T	F	Medicago minima	97	2	39	+	97	6	93	4	23	+	.	.	76	1	12	+	93	4	85	1	100	4	99	3	63	1	.	.	89	1	37	+	41	+	99	8	94	4	.	.	93	2	17	+
Ko	T	F	Trifolium campestre	97	2	55	+	59	2	100	6	96	1	.	.	93	2	77	1	96	2	9	+	43	+	87	2	72	1	.	.	81	1	85	1	3	+	85	4	96	5	1	+	92	1	82	1
Ko	T	H	Cerastium semidecandrum	61	1	11	+	81	1	87	1	17	+	.	.	25	+	63	1	89	1	.	.	83	1	91	2	4	+	.	.	31	+	63	1	.	.	89	1	89	2	.	.	62	+	58	1
Ko	T	G	Vulpia myuros	41	1	37	+	8	+	79	1	.	.	.	.	16	+	40	1	35	1	7	+	28	+	68	1	3	+	1	+	13	+	17	+	2	+	57	1	73	2	1	+	24	+	53	2
Ko	T	H	Saxifraga tridactylites	12	+	1	+	40	+	4	+	8	1	.	.	.	.	.	.	19	+	.	.	41	+	16	+	11	1	.	.	.	.	.	.	.	.	49	+	25	+	.	.	.	.	.	.
Ko	T	H	Alyssum alyssoides	1	+	1	+	4	1	3	1	8	1	.	.	4	+	.	.	.	.	.	.	.	.	1	+	1	1	.	.	.	.	.	.	.	.	1	+	1	+	1	+	3	+	.	.
Ko	T	H	Veronica verna	5	1	.	.	1	+	.	.	3	1	.	.	.	.	.	.	1	+	.	.	1	+	5	+	7	1	.	.	.	.	.	.	.	.	.	.	9	+	.	.	.	.	5	1
Ko	T	G	Phleum arenarium	.	.	.	.	.	.	1	+	.	.	.	.	.	.	1	+	.	.	1	+	4	+	5	1	.	.	.	.	.	.	.	.	.	.	1	+	3	+	.	.	.	.	1	+
Ko	H	H	Hieracium pilosella	1	1	3	2	4	1	4	+	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.	.	.	.
Ko	H	G	Corynephorus canescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19	1	7	+	7	+	24	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.

| | | |

	Degree of presence	Cover %	Vegetation type	p "Animal"	p "Animal*Vegetation type	p "Animal*Year(*Vegtype)" 2002	2003	2004	2005
Potentilla argentea agg.	x			0.0149					
Potentilla argentea agg.		x	A		0.0161				
Carduus nutans	x			0.0169					
Carduus nutans		x							0.0045
Arenaria serpyllifolia agg.		x					0.0252		
Arabidopsis thaliana	x							0.0450	0.0190
Petrorhagia prolifera		x	F		0.0116				
Agrostis capillaris	x		F				0.0190		
Berteroa incana		x	A		0.0084				
Erodium cicutarium agg.		x	F		0.0087				
Bromus hordeaceus	x		F		0.0154				
Bromus hordeaceus		x	A		0.0340				
Centaurea stoebe	x							0.0070	0.0061
Centaurea stoebe		x	F						0.0399
Trifolium arvense	x		F						0.0049
Trifolium arvense		x	F						<0.0001
Medicago falcata / M. x varia		x	A		0.0105				
Crepis capillaris	x			0.0470					
Conyza canadensis	x		F		0.0480				

Table 6.3. Plant species with significant results of the mixed linear model analyses either in their degrees of presence or in their mean cover values. The levels of significance (p) of the significant SAS-term with highest category are given. F: *Festuca duvalii*-subtype, A: Armerio-Festucetum trachyphyllae typicum.

Influence on the community structure

As shown in Table 6.2, the community structure, especially the diagnostic species composition of the two Armerio-Festucetum subtypes was not affected by the different grazing treatments. *Agrostis capillaris* was reduced in the case of donkey grazing from presence 48 % to 5 % in the *Festuca duvalii*-subtype.

Figure 6.3a demonstrates the development of the paddocks according to their floristic composition by means of detrended correspondance analysis (DCA). Although the eigenvalues are comparatively small, the DCA can be used as background information because many of the above-mentioned results are confirmed by this method of presentation. With regard to the arrangement of the plant species (Figure 6.3b), a decrease of species with a ruderal tendency with increasing values of the first axis and an increase of therophytes linear to the second axis can be detected. This is for example expressed by a negative correlation of *Berteroa incana* (r = -0.62) and a positive of *Festuca duvalii* (r = 0.61) along the first axis and

by a positive correlation of *Arenaria serpyllifolia* agg. (r = 0.62) along the second axis. Thus, the paddocks of the Armerio-Festucetum trachyphyllae typicum with a denser canopy are located at lower, those of the *Festuca duvalii*-subtype at higher values of the first axis. The general temporal development of all paddocks is strongly orientated along the second axis and to lesser extent along the first axis although some paddocks show a slightly divergent development. The dry year 2003 often leads to a sharp drop in the general trend which is mainly situated along the first axis in case of the donkey-grazed paddocks and leads to a regression along the second axis in case of the sheep-grazed paddocks of the *Festuca duvalii*-subtype. Most successively two-species-grazed paddocks as well as most of the only donkey-grazed ones show a regression tendency along the second axis in 2005.

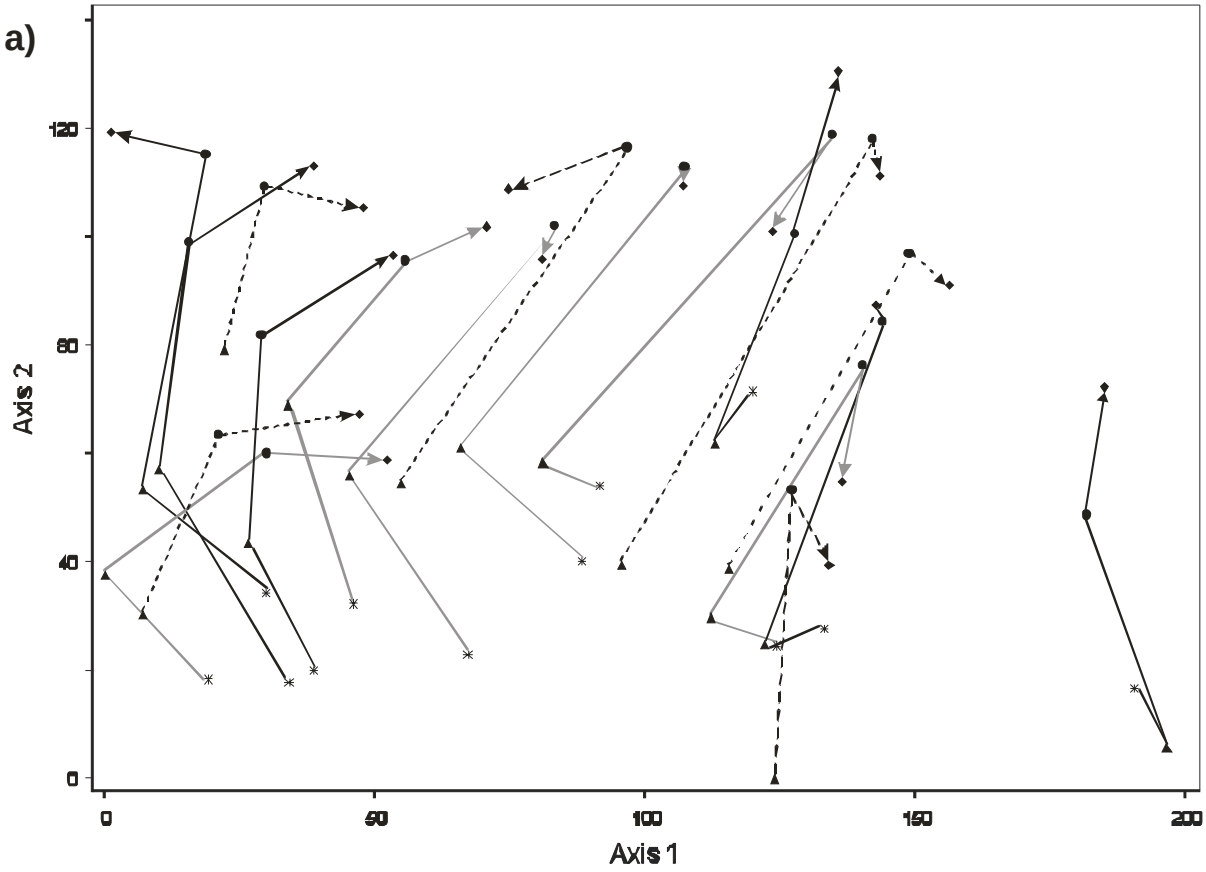

Figure 6.3a. DCA of the mean vegetation values for the investigated paddocks. Eigenvalues and lengths of gradients: First axis. 0.24, gradient: 2.0; second axis 0.10 gradient: 1.3; a) plots. Relevés from different years of the same paddock are connected, the arrow indicates the temporal development. Asterisks: relevés from 2002, triangle: 2003, circle: 2004, rhombus: 2005. Black solid line: sheep, grey solid line: donkeys, interrupted line: sheep and donkeys.

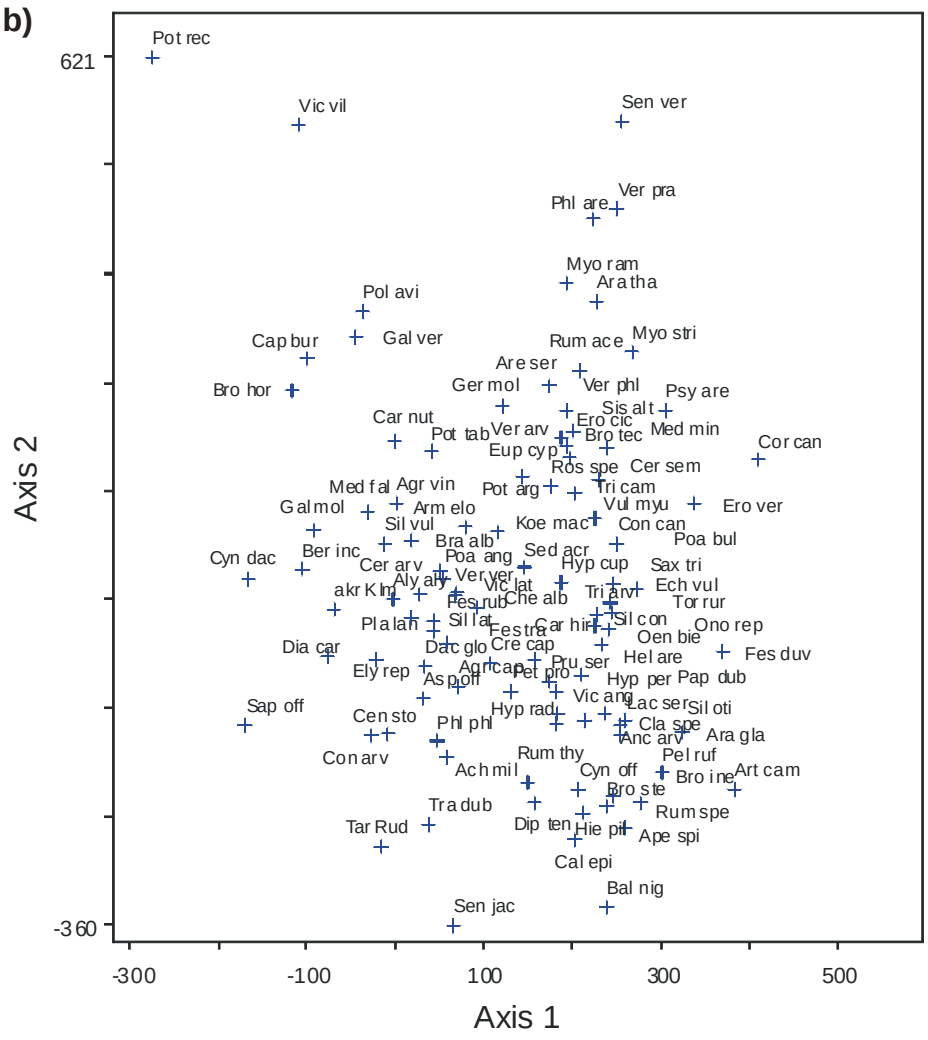

Figure 6b. species. Ach mil: *Achillea millefolium* agg., Agr cap: *Agrostis capillaris*, Agr vin: *Agrostis vinealis*, akr Klm: Acrocarpi, Aly aly: *Alyssum alyssoides*, Anc arv: *Anchusa arvensis*, Ape spi: *Apera spica-venti*, Ara gla: *Arabis glabra*, Ara tha: *Arabidopsis thaliana*, Are ser: *Arenaria serpyllifolia* agg., Arm elo: *Armeria maritima* ssp. *elongata*, Art cam: *Artemisiacampestris*, Asp off: *Asparagus officinalis*, Bal nig: *Ballota nigra*, Ber inc: *Berteroa in-cana*, Bra alb: *Brachythecium albicans*, Bro hor: *Bromus hordeaceus*, Bro ine: *Bromus inermis*, Bro ste: *Bromus sterilis*, Bro tec: *Bromus tectorum*, Cal epi: *Calamagrostis epigejos*,

Cap bur: *Capsella bursa-pastoris*, Car hir: *Carex hirta*, Car nut: *Carduus nutans*, Cen sto: *Centaurea stoebe*, Cer arv: *Cerastium arvense*, Cer sem: *Cerastium semidecandrum*, Che alb: *Chenopodium album* agg., Cla spe: *Cladonia* spec. Con arv: *Convolvulus arvensis*, Con can: *Conyza canadensis*, Cor can: *Corynephorus canescens*, Cre cap: *Crepis capillaris*, Cyn dac: *Cynodon dactylon*, Cyn off: *Cynoglossum officinale*, Dac glo: *Dactylis glomerata*, Dia car: *Dianthus carthusianorum*, Dip ten: *Diplotaxis tenuifolia*, Ech vul: *Echium vulgare*, Ely rep: *Elymus repens*, Ero cic: *Erodium cicutarium* agg., Ero ver: *Erophila verna*, Eup cyp: *Euphorbia cyparissias*, Fes duv: *Festuca duvalii*, Fes rub: *Festuca rubra*, *Fes tra: Festuca trachyphylla*, Gal mol: *Galium album*, Gal ver: *Galium verum* agg., Ger mol: *Geranium molle*, Hie pil: *Hieracium pilosella*, Hel are: *Helichrysum arenarium*, Hyp cup: *Hypnum cupressiforme*, Hyp per: *Hypericum perforatum*, Hyp rad: *Hypochaeris radicata*, Koe mac: *Koeleria macrantha*, Lac ser: *Lactuca serriola*, Med fal: *Medicago falcata* / *M.* x *varia*, Med min: *Medicago minima*, Myo ram: *Myosotis ramossisima*, Myo str: *Myosotis stricta*, Oen bie: *Oenothera biennis* s.l., Ono rep: *Ononis repens*, Pap dub: *Papaver dubium*, Pel ruf: *Peltigera rufescens*, Pet pro: *Petrorhagia prolifera*, Phl are: *Phleum arenarium*, Phl phl: *Phleum phleoides*, Pla lan: *Plantago lanceolata*, Poa ang: *Poa angustifolia*, Poa bul: *Poa bulbosa*, Pol avi: *Polygonum aviculare* agg., Pot arg: *Potentilla argentea* agg., Pot rec: *Potentilla recta*, Pot tab: *Potentilla tabernaemontani*, Pru ser: *Prunus serotina*, Psy are: *Psyllium arenarium*, Ros spe: *Rosa* spec., Rum ace: *Rumex acetosella*, Rum spe: *Rumex* spec., Rum thy: *Rumex thyrsiflorus*, Sap off: *Saponaria officinalis*, Sax tri: *Saxifraga tridactylites*, Sed acr: *Sedum acre*, Sen jac: *Senecio jacobaea*, Sen ver: *Senecio vernalis*, Sil con: *Silene conica*, Sil lat: *Silene latifolia* ssp. *alba*, Sil oti: *Silene otites*, Sil vul: *Silene vulgaris*, Sis alt: *Sisymbrium altissimum*, Tar Rud: *Taraxacum* sect. *Ruderalia*, Tra dub: *Tragopogon dubius*, Tri arv: *Trifolium arvense*, Tri cam: *Trifolium campestre*, Tor rur: *Tortula ruraliformis*, Ver phl: *Verbascum phlomoides*, Ver arv: *Veronica arvensis*, Ver pra: *Veronica praeox*, Ver ver: *Veronica verna*, Vic ang: *Vicia angustifolia*, Vic lat: *Vicia lathyroides*, Vic vil: *Vicia villosa*, Vul myu: *Vulpia myuros*.

Percentage of bare ground and cover of seedlings

As demonstrated in Figure 6.4, the percentage of bare ground increased throughout the investigated period. But only in the case of the estimates made shortly after the grazing period (September 2003, p = 0.015, and immediately after grazing 2004, p = 0.003) were significant differences between sheep and donkey grazing observed, while the combined grazing regime occupied an intermediate position.

The cover of seedlings was slightly not significantly different (p = 0.052 in 2004) between the three grazing regimes although a tendency towards a lower cover of seedlings in the case of sheep grazing can be detected in relation to the other treatments (see Figure 6.5).

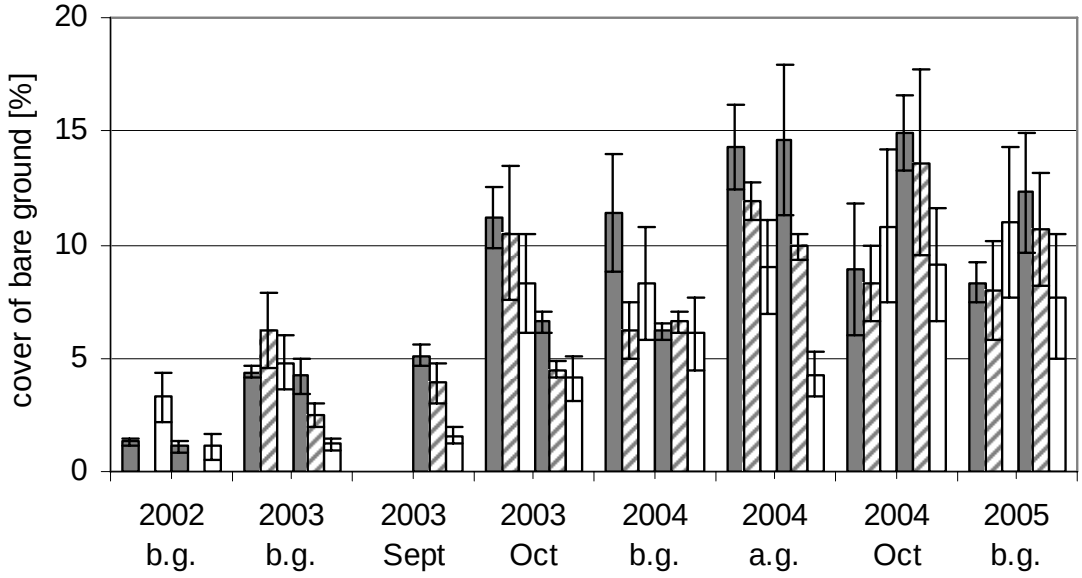

Figure 6.4. Cover of bare ground for donkey grazing (grey), mixed treatment (grey + white) and sheep grazing (white). b.g.: before grazing, a.g.: after grazing, Sept: September, Oct: October. Left bars of each point of time: *Festuca duvalii*-subtype, right bars: Armerio-Festucetum trachyphyllae typicum. Error: standard error.

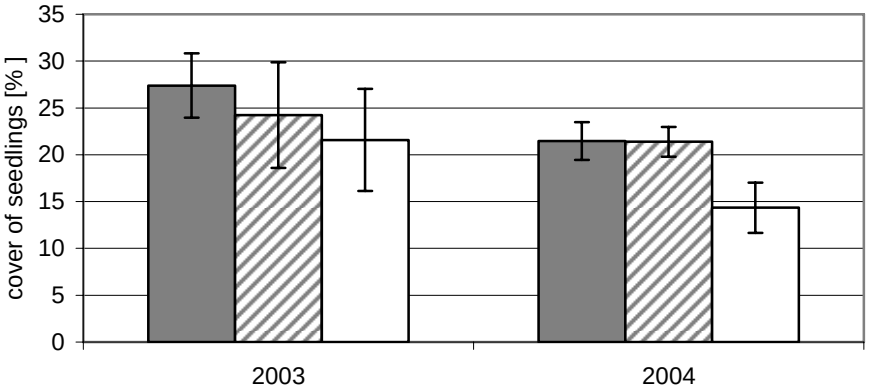

Figure 6.5. Mean cover of seedlings for donkey grazing (grey), mixed treatment (grey + white) and sheep grazing (white). Error: standard error.

Vegetation of special sites related to donkey grazing

The differences between degrees of presence at the special sites and the controls of the investigation of 2003 and 2004 as well as of the analyses of the faeces plots in November 2004 (after 15 weeks) and in June 2005 (after 45 weeks) are shown in Table 6.4. There are some species with higher abundance at the disturbance sites (positive values), others with higher abundance at the control plots (negative values). No species was clearly supported by faeces accumulation sites but, e.g., *Potentilla argentea* agg. and the Red List species *Armeria maritima* ssp. *elongata* had lower degrees of presence at the faeces sites than at the control plots. In the case of the urine accumulation sites, especially *Bromus hordeaceus* and *Chenopodium album* agg. were of higher presence while *Agrostis capillaris, Rumex acetosella* and again *Armeria maritima* ssp. *elongata* reached higher presence values at the control plots. In the case of the disturbances associated with bare ground (wallows and scratch-sites), especially the "gap-species" *Verbascum phlomoides*, *Silene conica*, *Arenaria serpyllifolia* agg., *Erodium cicutarium* agg., *Potentilla argentea* agg., *Sisymbrium altissimum, Sedum acre* and *Diplotaxis tenuifolia* benefited from an increase of bare ground while on the other hand the indicator species of more consolidated stages, e.g., *Poa angustifolia, Cerastium arvense* and *Achillea millefolium* agg. were restricted to the control plots. The bryophytes *Hypnum cupressiforme* var. *lacunosum* and *Brachythecium albicans* usually had a higher presence values at the control plots (negative values) - regardless of the kind of disturbance. The number of species showed a tendency towards decreasing plant species richness on the nutrient-enriched plots (faeces- and urine-accumulation sites), indicated by negative values, and an increase on the bare-ground plots (wallows and scratch-sites) in relation to the controls, indicated by positive values.

	1) Investigation of special sites								2) Faeces-Exp.			
Year	2003	2004	2003	2004	2003	2004	2003	2004	2004	2005	2004	2005
Plot type	W	W	S	S	F	F	U	U	F	F	U	U
Number of compared pairs	3	3	4	4	9	9	3	3	12	11	6	4.0
Difference in the number of species	4	-1	3	2	-1	-2	-3	-4	-2	-1	-3	-2.8
Mainly increase												
Chenopodium album agg.	33	33	*	-25	.	11	100	33	.	.	.	.
Erodium cicutarium agg.	33	*	25	50	-11	11	*	*	-17	18	*	50
Sisymbrium altissimum	*	33	75	*	11	-11	-33	67	.	.	.	25
Elymus repens	.	33	*	-25	11	22	*	*	*	-9	17	50
Bromus hordeaceus	*	*	-50	25	11	*	.	.	17	-9	83	75
Vulpia myuros	*	33	25	*	22	*	.	.	*	9	*	*
Convolvulus arvensis	.	.	.	.	11	11	*	33	.	18	.	*
Bromus tectorum	67	*	-25	*	-11	22	.	33	.	9	.	.
Verbascum phlomoides	33	*	75	75	*	22	-33	33	-8	*	-33	-25
Diplotaxis tenuifolia	33	33	50	.	.	11	-33	.	.	.	.	.
Asparagus officinalis	33	33	25	.	-11	.	.	.	.	.	.	.
Oenothera biennis s.l.	*	.	25	25	.	*	.	.	.	.	.	.
Polygonum aviculare agg.	.	33	.	.	.	.	.	.	8	.	.	.
Ononis repens	.	.	*	.	11	*	.	.	.	.	.	25
Cynodon dactylon	*	*	.	.	*	*	.	.	8	*	*	*
Medicago falcata x varia	33	33	25	*	11	*	*	*	-8	-9	-17	*
Mainly decrease												
Hypnum cupressiforme	.	-33	-25	.	.	-44	-33	.	-42	-55	-50	-75
Rumex acetosella	*	*	*	*	-33	-22	*	-33	*	-9	-17	-50
Achillea millefolium	-33	-33	-25	-50	11	-11	.	-33	8	-18	-17	.
Koeleria macrantha	-33	-67	25	*	-11	-11	*	-67	-8	*	-17	-50
Arabidopsis thaliana	.	-33	.	.	.	-11	.	.	.	.	.	.
Armeria maritima ssp. elongata	.	.	25	-25	-33	-44	-33	-67	8	*	.	.
Poa angustifolia	-33	*	-50	-25	-33	*	-67	33	-33	*	-33	*
Plantago lanceolata	-33	.	*	*	22	*	-33	*	-8	-18	-17	-50
Brachythecium albicans	.	-33	-25	-25	.	-44	.	-33	.	.	.	.
Sedum acre	67	.	25	.	*	.	-33	-33	-8	-18	-17	-25
Berteroa incana	33	*	-50	*	-22	-22	*	-33	-8	-9	*	*
Agrostis capillaris	.	.	.	.	-11	.	-33	-33	.	*	.	-25
Potentilla argentea agg.	.	33	*	50	-33	11	-33	-33	-33	*	-50	-25
Cerastium arvense	-33	-33	-25	-25	*	-22	-33	33	*	*	*	.
Petrorhagia prolifera	.	.	*	25	*	-11	.	-67	-8	9	-17	.
Carduus nutans	.	.	25	-50	.	*	33	.	-8	-9	-17	.
Vicia lathyroides	.	-33	-25	25	*	-44	.	-33	.	18	.	-25
Festuca trachyphylla	*	-100	-25	*	11	*	.	.	-42	-9	17	-25
Saxifraga tridactylites	.	-33	-25	.	.	.	.	-33	.	.	.	.
Silene conica	*	33	.	75	-22	-11	.	.	.	-18	.	-25
Slight or no differences												
Veronica arvensis	33	-67	25	-25	22	*	*	-33	8	9	.	.
Trifolium arvense	.	33	.	25	-11	*	-33	33	-8	9	.	*
Cerastium semidecandrum	.	*	25	25	11	-44	-33	.	.	-27	.	.
Silene latifolia ssp. alba	33	33	-25	*	*	-22	.	.	8	*	-17	*
Trifolium campestre	33	33	25	*	*	*	.	.	.	-18	.	-25
Myosotis ramosissima	.	.	.	-25	22	11	.	-33	.	9	.	-25
Rumex thyrsiflorus	.	.	-25	-25	11	11	.	.	.	.	17	.
Medicago minima	.	*	-25	*	.	-33	.	*	25	*	*	*
Vicia angustifolia	.	.	-25	25	.	*	.	-33	.	-9	.	*
Geranium molle	.	-33	*	*	*	*	*	-33	8	9	-33	.
Conyza canadensis	*	.	50	.	.	.	.	.	.	-9	.	.
Crepis capillaris	.	.	.	.	.	-11	.	-33	.	9	.	.
Phleum phleoides	.	*	.	.	-22	-22	.	*	.	9	.	.
Poa bulbosa	.	33	.	.	.	.	.	.	.	.	.	.
Acrocarpi	.	.	.	25	.	.	.	.	.	.	.	.
Cynoglossum officinale	.	.	25	.	.	.	.	.	.	.	.	.
Saponaria officinalis	.	.	25	.	.	.	.	.	.	.	.	.
Agrostis vinealis	.	.	.	.	.	.	.	.	.	9	.	.
Myosotis stricta	.	.	.	.	.	-11	.	.	.	.	.	.
Helichrysum arenarium	.	.	.	.	.	.	*	-33	.	.	.	.
Bromus sterilis	.	.	.	.	.	.	-33	*	.	.	.	.
Centaurea stoebe	33	*	25	*	11	22	67	-33	-8	-18	-17	-50
Arenaria serpyllifolia	*	*	75	50	-11	11	*	*	-8	9	.	*
Echium vulgare	33	*	*	25	-11	22	*	*	-8	.	.	.
Carex hirta	33	.	.	.	*	*	*	-33	8	*	-17	*
Potentilla tabernaemontani	*	.	75	.	-11	.	.	.	.	.	.	.
Tragopogon dubius	.	.	-25	*	.	11	.	.	.	.	.	.
Tortula ruraliformis	.	-67	25	*	.	.	.	.	.	.	.	.
Anchusa arvensis	.	.	.	.	.	*	*	*	.	.	.	.
Capsella bursa-pastoris	.	*	.	.	.	.	.	.	.	.	.	.

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Table 6.4. Differences of the percentual degree of presence for each species between control plot and special sites as well as between total species number of control and special sites. Positive values: higher abundance/species number at the special sites, negative values: higher abundance/species number at the control plots. *****: No difference between control plots and special sites; dot: species was not present at both plots. The relevés of two different experiments were used: 1) Investigation of special sites resulting from donkey grazing 2002. Relevés from summer 2003 and summer 2004. W: wallow, S: scratch-sites, F: faeces accumulation site, U: urine accumulation site 2) Investigation of faeces sites 2004: Relevés from November 2004 (after 15 weeks) and June 2005 (after 45 weeks). F, U as in 1).

Phytomass of the faeces plots

Figure 6.6 shows the total phytomass of faeces-plots, urine-plots and control-plots in autumn 2004 (after 15 weeks) and summer 2005 (after 45 weeks). In 2004, because there was a huge amount of necromass at the urine plots, this was sampled separately. Including the necromass, phytomass at the faeces-sites is significantly lower than that of the control ($p = 0.021$) and of the urine plots ($p = 0.010$). Without considering the necromass, only the comparison between faeces plots and control plots is significant ($p = 0.025$). In summer 2005, no significant difference between the three plot types can be detected.

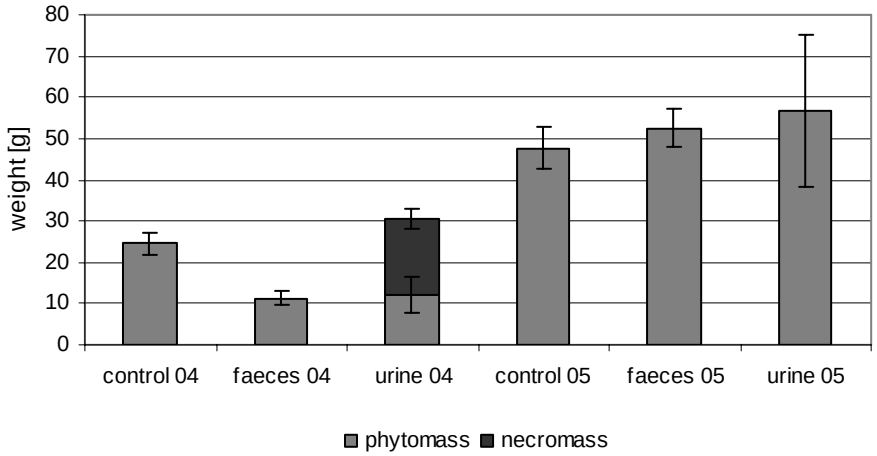

Figure 6.6. Weight of the mown phytomass/necromass at donkeys' faeces plots, urine plots and control plots in November 2004 and June 2005. Error: standard error.

Nitrogen input at faeces accumulation sites

Altogether, the replicated 20 cm x 20 cm faeces-plots were very heterogeneous. On the basis of the faeces mass per plot (mean = 50 g, SE = 4.3 g) and the analysed percentage of nitrogen (mean = 1.8 %, SE = 0.08 %), the amount of nitrogen per plot was estimated. No significant decrease of the amount of nitrogen in relation to the beginning (t_0) was detectable: the mean value for nitrogen at the donkeys' faeces accumulation sites throughout all sampling times was 0.89 g N per 20 cm x 20 cm plot (i.e. 223 kg N * ha^{-1}). The mean cover of faeces after the grazing period 2004 was 4 % (SE = 0.5 %). Therefore, within one grazing period, 4 % of the paddock area was affected by a nitrogen input of 223 kg * ha^{-1}.

Discussion

Influence of the year

The results have shown the strong impact of the variable "year" on most investigated parameters. Also Hiernaux (1998) and Sternberg et al. (2000) found that the influence of climatic conditions on vegetation parameters was much stronger than the effects of the grazing treatments. A significant effect of dry and wet years was also observed by van Staalduinen (2005) by investigating Przewalski horse grazing in the Mongolian steppe. Given that other investigations of our own in this period and area produced the same findings (Schwabe et al. unpublished data), we conclude that they are mainly due to the extraordinary climatic conditions and only to a smaller degree are the result of a repetition of the measurements. Remarkably, for different climatic conditions, i.e. within different years, different variables become significant. Those variables that are significant for several years can be regarded as consistent grazing effects of the investigated animals that are extremely robust against environmental changes. Others are typical for dry conditions (2003) or for compensatory effects (2004). Hence the investigation also concerns the question of the treatments' suitability for different environmental conditions. First of all, these results emphasise the need for long-term ecological studies because different conclusions can be drawn for different climatic conditions. But as the year 2003 is sometimes regarded as a model year for future climatic conditions within a global change scenario (Schär et al. 2004, Meehl & Tebaldi, 2004), the results can also be regarded as trend-setting for future climatic conditions. The difficulty of detecting grazing effects under drought conditions was also reported by Peco et al. (in press).

Effects on the plant community structure

The summarised significant differences between the animals show that besides some changes in species presence and abundance, donkeys reduce the cover of graminoids, bryophytes and litter more intensively than sheep and that on the other hand the number of species, especially therophytes, is higher in case of donkey grazing. This can easily be explained by the different animals' behaviour and their general grazing preferences. Nearly all of the favoured species are seed bank species, which germinate when the soil has been disturbed.

Previous studies have also shown that donkeys graze more intensively on graminoids than do sheep (Süss et al. submitted). As a consequence of the grass reduction, less litter is produced, the canopy is opened and competition for therophytes decreases (Kooijman & van der Meulen 1996). Comparable investigations in wet ecosystems with horses and cattle also found a

higher number of species in case of non-latrine horse-grazed areas and intermediate for mixed management and cattle (Loucougaray et al. 2004). The decrease of *Agrostis capillaris* is an additional indication that potentially dominant graminoid species are reduced by donkey grazing.

Also the reduction of *Medicago falcata / M.* x *varia* and the increase of *Potentilla argentea* agg. in case of donkey grazing can be interpreted as consequences of the grazing preferences. Although donkeys as well as sheep prefer *Medicago falcata / M.* x *varia* to a high degree (Süss et al. submitted), sheep prefer the leaves and reject the stem while donkeys grub the whole plant and also graze the roots of this species. In the long run, destructive herbivory as described by Rockwell et al. (2003) is expected for *M. falcata / M.* x *varia*. with donkey grazing. After three treatment years, *M. falcata / M.* x *varia* decreased in cover but is not yet influenced in its abundance.

Potentilla argentea agg. is supported by donkey grazing in its degree of presence as well as in its mean cover values. This is a plant species which is supported by two functional impacts. On the one hand it is not grazed by donkeys (Süss et al. submitted) and therefore it profits indirectly from decreasing competition; on the other hand, the analyses of the wallows and scratch sites have shown that this seed bank species (Eichberg et al. 2006) is more common here than on the control plots.

The plant species with higher abundance in the gaps than on the control plots are often therophytes, whereas hemicryptophytes and chamaephytes are typical for the more consolidated controls. Hence the increase of therophytes in comparison to the sheep-grazed paddocks can be explained by the equids' habit of rolling and scratching and thus producing regeneration niches.

The analysis of the increase of bare ground has shown that a remarkable difference between sheep and donkey grazing is observable only immediately after the grazing has occurred. But the absence of significance at the other times is not only a consequence of an increased cover of therophytes at the donkey-grazed paddocks, where available regeneration niches were quickly colonised and thus the percentage of gaps decreased rapidly, resulting in an increased cover of therophytes. Instead, the data show that especially at the Armerio-Festucetum trachyphyllae typicum, also during the post-grazing period, a further increase of bare ground was observed. This can only partially be explained by phenological aspects of a decrease of phytomass in autumn. Instead, it is due to the intensive rabbit activity, especially in 2003 and 2004. The rabbits frequently grub and scratch at sites where small disturbances have occurred but were not observed to burrow at large disturbance-sites such as wallows – maybe due an

increased compactness of the soil at these sites. This effect was less intense at the *Festuca duvalii*-subtype. Here, the cover of bare ground was high after grazing 2004 for donkeys and for sheep followed by donkeys. By October it had decreased at the donkey- and successive two-species-grazed paddocks but remained the same at the sheep-grazed sites. This effect is likely to be reflected in the observed higher number of therophytes at the donkey- and successive two species-grazed paddocks in 2005.

Influence of faeces accumulation sites

The analyses have shown a strong nitrogen input (223 kg N * ha^{-1}) at donkeys' faeces accumulation sites, which can be compared to a very intensive fertilisation impact (Scheffer & Schachtschabel 2002). Also for other equids it was shown that the percentage of latrine-affected sites increased throughout the years (Kolter et al. 1999). The nitrogen input results from the previous nitrogen extraction by grazing on the whole paddock. Therefore a huge heterogeneous horizontal distribution pattern of nitrogen by means of grazing is observed. The decomposition of the faeces nitrogen content is very slow and even after 45 weeks, no decrease of nitrogen was detectable. Thus, the conclusion can be drawn that leaching losses of nitrogen must be small, and although nitrogen was obviously not taken up by the plants immediately, after a longer period spots of ruderalisation may occur due to a fertilisation effect.

In contrast to Loucougaray et al. (2004), who found a significant increase of canopy height at horse latrines, the amount of phytomass was significantly lower at the faeces and urine plots in autumn 2004 (t_4) - probably due to the mechanical and/or chemical destruction of the actual vegetation. Other studies within the same ecosystem have shown an increase of phytomass after two years of NPK addition (100 kg N*ha^{-1}*a^{-1}) and after 4 years of nitrogen applied solely (100 kg N*ha^{-1}*a^{-1}), accompanied by a significant change of vegetation parameters (Süss et al. in prep.) The fact that in the case of the donkey faeces no significant increase of phytomass was detected can be due to the comparatively slow degradation of nitrogen. Also the rather short time-span after a single nutrient impact accompanied by a mechanical destruction of the actual phytomass can be the reason for the different results in that investigation. Nevertheless, the investigated donkey faeces-sites were influenced in their plant species composition. Often ruderal plant species are supported, as evidenced for example by the higher abundance of *Chenopodium album* agg. or *Sisymbrium altissimum*. Red List species which are often restricted to nutrient-poor sites were usually of higher presence at the

controls. A decrease of plant species richness at equids' latrine areas has been pointed out by Fleurance et al. (2001) and Loucougaray et al. (2004).

The ruderalisation trend at the donkeys' faeces sites can be discussed from different points of view. Although the plant species at these plots are often not endangered, for many endangered animal species – for example wild bees (Hymenoptera, Apoidea) - these are essential resources. In that case, the combination of flowers (e.g. *Centaurea stoebe, Berteroa incana* and *Sisymbrium altissimum* as very important wild bee pollen resources) and an open habitat (important, e.g., for nesting sites) as a consequence of grazing is essential (Beil & Kratochwil 2004). Nevertheless, the typical floristic structure of the Armerio-Festucetum trachyphyllae should be protected.

General discussion and conclusion

In general, extensive grazing has proved to be an adequate method of maintaining and increasing plant species richness in many ecosystems (Taddese et al. 2002, Hellström et al. 2003, Schwabe & Kratochwil 2004). In our case, the conclusion can be drawn that all three investigated grazing regimes are suitable methods with which to manage and develop sand ecosystems with site-specific diversity. The influence of sheep grazing is less intensive but more continuous than that of donkey grazing, and shows the same main effects (reduction of graminoids and litter, increase of herbs and bare ground). Donkeys are processors of a special vegetation pattern with great variability in space and time. Hence, donkey grazing is an appropriate management method to obtain strong effects within a short time span. But it should not be repeated too often, because otherwise a re-ruderalisation of large parts of the paddocks can be the consequence as shown in Figure 6.3. The successive combination of both species usually achieves intermediate results. In contrast to the analysis of the grazing preferences (Süss et al. submitted), the effects on the vegetation are not enhanced by two-species grazing.

This can be different for larger paddocks and a more ruderalised vegetation composition such as fallow land. In these cases, successive two-species grazing may be a very suitable method for developing communities with high conservation values. In the case of plant communities which already have this value, such as the investigated ecosystem, extensive sheep grazing is a very adequate tool (Schwabe et al. 2004) and should be the main management method. Donkey grazing can be used rarely and additionally to reduce dominant grass species and to create a greater number of gaps, but should not be repeated over several years.

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Chapter 7:
General discussion

Increasing nitrogen depositions as well as severe changes in agricultural land-use are known to cause an increase of ubiquitous competitive and ruderal plant species and a decrease of site-specific stress-tolerators in sand ecosystems. The aim of this thesis was to develop a model of successional pathways for inland sand ecosystems as a basis for elucidating the interrelationship between nutrient addition, diversity and productivity. Since these ecosystems depend on a grazing impact, the effects of three different grazing regimes (sheep grazing, donkey grazing, sheep followed by donkey grazing) as measures for nature conservation management were focussed. In this chapter the results of the different experiments are discussed in context and synthesised conclusions for ecological processes in calcareous inland sand ecosystems are drawn. A schematic description of the main conclusions is provided in Figure 7.1 and discussed in the following.

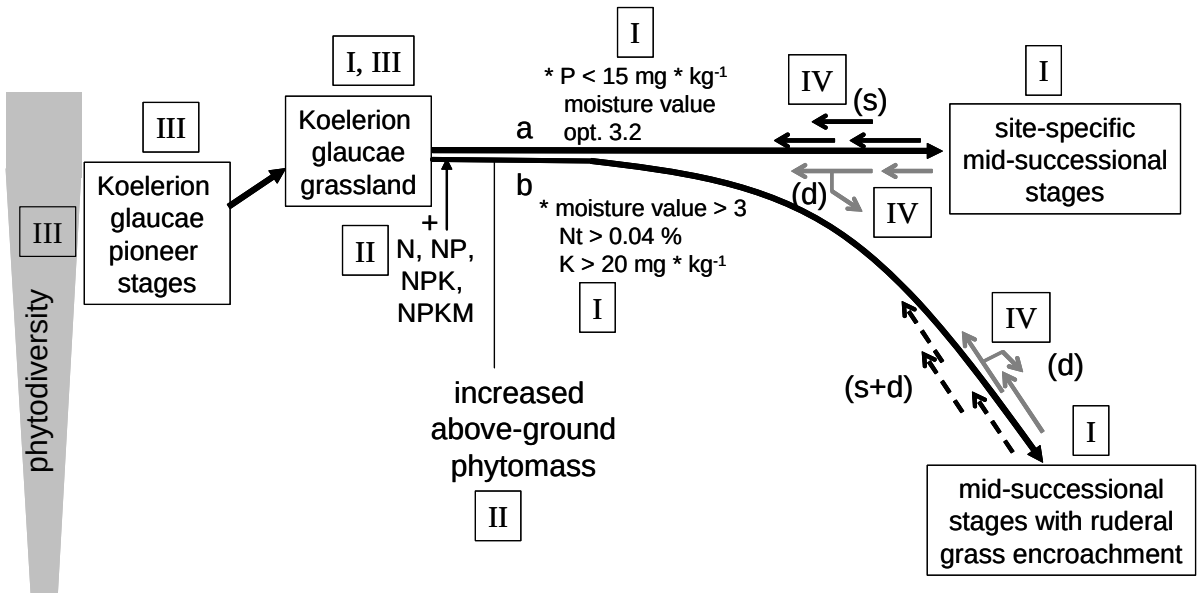

Figure 7.1. Successional model of sand ecosystems with a presentation of the conclusions derived from the different chapters of the thesis. The Roman numerals refer to the topics discussed below. a: non-ruderalisation pathway, b: ruderalisation pathway, *: values for Allio-Stipetum community. s: sheep grazing, d: donkey grazing, s+d: successive sheep and donkey grazing. The number of the arrows indicate a repeated measurement.

Succession (I)

The successional model developed in **Chapter 2** revealed that nutrient contents and water availability of the soil are decisive for the course of succession. As demonstrated in Figure 7.1 for the case of spontaneous succession, only areas with very low phosphate contents < 15 mg * kg^{-1} show the capacity to develop site-specific mid-successional vegetation types characterised by the presence of endangered species, and hence have high conservation values as threatened habitats (pathway a).

In general, the influence of phosphate for successional development and for species composition has long been underestimated. Only very recently has the importance of phosphate been considered. For moist grassland Wassen et al. (2005) pointed out that enhanced phosphorus is more likely to be the cause of species loss than is nitrogen enrichment, while Kooijman et al. (1998) propose a co-limitation of phosphate and nitrogen for coastal calcareous sand ecosystems. But most studies focussed on nitrogen as the main limiting factor in terrestrial systems and as the most important driving factor for succession (e.g. Olff et al. 1993, Chapin III et al. 2002). As demonstrated in **Chapter 2**, an increased nitrogen and potassium supply of the soil (N_{total} > 0.04 %, K > 20 mg * kg^{-1}, 0-10 cm soil depth) can indeed lead to ruderalisation and encroachment of the tall grass species *Calamagrostis epigejos* (see Figure 7.1, pathway b). Therefore it can be concluded that old fields, which were formerly fertilised, represent areas for ruderal grass-encroachment characterised by low conservation value. Here, management methods are necessary to direct the ruderal successional pathway into the non-ruderalised direction with higher diversity of site-specific plant species.

Besides limiting values of soil phosphate content, water availability is also thought to be decisive for the existence of successional pathways (**Chapter 2**). At very dry sites which are characterised by mean Ellenberg moisture values < 3 (Ellenberg et al. 1992) ruderal grass-encroachment seems to be impossible. This is probably due to different life strategies. As described above, the site-specific plant species are mainly stress-tolerators according to Grime (1979) while the dominant tall grass species are mainly competitors often accompanied by ruderals. When the nutrient and water supplies are enhanced, competitors and ruderals become dominant while stress-tolerators are restricted to dry and nutrient-poor sites as a matter of competition.

As in natural systems, water supply cannot directly be influenced by management methods, so that tools of nature conservation must be employed to reduce nutrient availability in these areas by phytomass extraction. Indirectly, a decrease of tall grasses can also lead to a decrease

of litter and humus and thus reduce field capacity of the soils by reducing the amount of small particles.

Nutrients (II)

Within the experimental approach described in **Chapter 3** the impact of nutrient addition upon early successional stages was analysed. As shown in Figure 7.1, phytodiversity and community structure were not found to be influenced during the early successional stages within four years of treatment. The lack of influence in **Chapter 3** is supposed to be restricted to early successional stages and limited time-span. With reference to **Chapter 2**, soil nutrient content is likely to gain in importance during succession as suggested in Figure 7.1.

Nearly all species benefit from a nutrient input, and phytomass was found to increase with N, NP, NPK or NPKM addition and is thus limited by nutrient supply. But even in the case of an enhanced nutrient supply phytomass production remains very low and is well below the mean value for grassland phytomass production of 200-5000 g * m^{-2} (Whittaker 1970). As Chapin et al. (1986) pointed out, due to the typical species composition of low-productivity sites, responses to nutrient addition are limited, so that even with intensive nutrient addition these areas are characterised by low productivity.

For early successional stages phosphate applied solely does not have significant effects - except on Fabaceae; however, if the nitrogen supply is sufficient, other nutrients such as phosphate or potassium gain in importance. Therefore, in the Koelerion glaucae vegetation complex mainly nitrogen is a limiting factor and phosphate at most becomes important if nitrogen supply is guaranteed. But in mid-successional stages (**Chapter 2**), phosphate is decisive for successional pathways, and mineral nitrogen content - which is enriched during succession (Gleeson & Tilman 1990) - is of subordinate importance. The low-dosage nitrogen approach (n) as an approximation of atmospheric nitrogen deposition was not found to have any impact on the investigated variables (**Chapter 3**). Therefore it can be concluded that in contrast to other investigations in coastal systems (Kooijman et al. 1998), in the ecosystem investigated here atmospheric nitrogen deposition does not significantly influence the vegetation of early successional stages.

By analysing the results obtained in different years, in **Chapter 3** water was also concluded to be an important limiting factor of early successional stages. Not only the phytomass production but also species composition can inferred to be highly affected by water availability. This again supports the above-mentioned conclusion that the site-specific plant

species are mainly stress-tolerators which are adapted to dryness, whereas ruderals and competitors are presumably not able to present a major challenge under dry conditions.

Productivity and phytodiversity (III)

The investigation of the productivity-diversity relationship revealed a strong dependence on the year and on scale (**Chapter 4**). For broad-scale analyses, a hump-shaped relationship between productivity and plant species richness was found. Perhaps the scale dependence is typical of these sandy grassland stages, as it was not found in other investigations (Allock & Hik 2003, Roscher et al. 2005). Due to the high phytodiversity of the investigated habitat types maximum plant species richness cannot be reached at fine-grain scale because of a limited plot size. Therefore the negative relationship at fine-grain scale is probably an artefact sensu Oksanen (1996).

Hence, the relationship found for the investigated system would be expected to be hump-shaped with highest species number at Koelerion glaucae grassland stages (see Figure 7.1), lower at pioneer Koelerion glaucae plots and lowest at consolidated Armerio-Festucetum trachyphyllae grassland. The latter will develop in the presence of top-soil acidification, and the results of all experiments showed that phytodiversity of this vegetation type is slightly lower than that of Allio-Stipetum plots but clearly higher than that of *Calamagrostis epigejos*-dominance stands. Many authors described a hump-shaped relationship (e.g. Tilman 1982, Abramsky & Rosenzweig 1984, Rosenzweig 1992, García et al. 1993, Tilman & Pacala 1993, Huston & DeAngelis 1994). But usually these models apply over a large ecological amplitude, ranging from very low to high productivity. Thus, our investigation area can be integrated into the ascending part of the hump-shaped model and we actually should expect a positive relationship between diversity and productivity.

The fact that in the experiment described in **Chapter 4** the Koelerion glaucae grassland stages are the sites with highest plant species diversity, and also with the largest number of endangered plant species, emphasises the ecological significance of management methods to preserve and to restore those habitats. As it was proved in **Chapter 2**, spontaneous succession can lead to low-phytodiversity sites. Since the investigation was carried out at a sheep-grazed ecosystem, the grazing impact is essential and possibly the main cause of the hump-shaped relationship. Aarssen (2001) stated that the heterogeneity of the environment, the availability of species and the opportunity for facilitation cause the unimodal shape of the response curve. All these factors are remarkably influenced by grazing (**Chapters 5** and **6**).

Opposed to these conclusions, the results displayed in **Chapter 4** show that livestock nutrition, i.e. crude protein content is positively correlated with productivity. This leads to a dilemma between ecological and economical aspects. One possible way to combine adequate livestock nutrition and targets of nature conservation would be that the sheep graze in alternation between these low-productivity sites and more productive nutrient-rich areas with low phytodiversity. This concept is the central aspect of a "Testing and Development" project funded by the "Federal Agency for Nature Conservation" (Germany) from 2004 to 2008.
The second possibility would be to use different livestock species as is discussed in **Chapters 5** and **6**. Here donkeys were used as grazing animals, and it was demonstrated by Lamoot et al. (2005a) that donkeys are sufficiently nourished by the scarce vegetation of sand ecosystems.

Grazing (IV)

Since numerous studies had already pointed out the effectiveness of extensive sheep grazing for the management of other low-productivity systems (Hellström et al. 2003) as well as for our model system (Stroh et al. 2002, Schwabe et al. 2004, Schwabe & Kratochwil 2004), this study focussed on a comparison between sheep grazing, donkey grazing (representatives of equids) and mixed treatment as management tools for inland sand ecosystems. This approach can also be regarded as a model for a comparison between ruminant and non-ruminant grazing. Similarly, in wet ecosystems combined cattle and horse grazing is of some importance (Menard et al. 2002, Loucougaray et al. 2004, Lamoot et al. 2005b).
As was revealed in **Chapter 5**, sheep and donkeys complement each other well with regard to their diet preferences, and maximum phytomass extraction is reached in case of successive sheep and donkey grazing. Especially plant species with high fibre contents, for example graminoids, are more intensively grazed with the two-species treatment than with only sheep grazing. The effects of the three grazing regimes on the vegetation of sand ecosystems are described in **Chapter 6**. It turned out that donkeys produce a high variability of microsites and create gaps to a great extent. According to Fynn et al. (2004) and Lepš (2005), disturbance may be an important determinant of diversity by modifying resource availability and the abundance and vigour of competitive dominants. But when donkeys graze small parts of the paddock, a nitrogen impact of 223 kg * ha^{-1} can be observed - accompanied by phosphate and potassium as other remarkable nutrients at excreta sites (Brenner at al. 2004). As demonstrated in **Chapter 3**, this can lead to a phytomass increase, and although plant species composition of early successional stages seems not to be affected by a nutrient input,

during succession an increased nutrient supply can lead to ruderalisation (**Chapter 2**). Therefore donkey grazing induces positive effects from the viewpoint of nature conservation, such as gap creation (**Chapter 6**), but due to the tendency towards partial ruderalisation of the paddocks it is no adequate substitute for sheep grazing. Apart from the creation of special sites in the case of donkey grazing, vegetation is not essentially differently affected by the three grazing regimes (**Chapter 6**) and, e.g., an increase of the cover of herbs, a decrease of the litter layer, and increasing numbers of therophytes were achieved with all approaches.

The effects of the three investigated grazing regimes in case of different successional pathways are demonstrated in Figure 7.1. Sheep grazing (s) is ideal for the management of relatively intact ecosystems to prevent succession. To allow for adequate animal nutrition (**Chapter 4**) sheep should graze these ecosystems in alternation with areas characterised by higher productivity and higher crude protein contents. Donkey grazing (d) is ideal for consolidated stages because intensive gap creation occurs. But this method cannot be recommended as a repetitive management method because parts of the paddocks can develop in a ruderal direction (see Figure 7.1). With reference to the diet preferences (**Chapter 5**) it can be concluded that sheep followed by donkey grazing (s+d) would be the ideal management tool for ruderal sites with grass-encroachment.

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Summary

Inland sand ecosystems are among the most threatened habitats in Central Europe. In recent decades, a decrease of site-specific plant species accompanied by a ruderalisation tendency was observed. This has often been explained by the influences of an enhanced nutrient supply and more widely distributed sites of spontaneous succession due to the abandonment of extensive land-use.

The aim of this thesis was to develop a successional model of inland sand ecosystems as a basis for elucidating effects of ecosystem functioning, such as the phytodiversity-productivity relationship, and to simulate effects of an increased nutrient supply. As these habitats depend on a grazing impact, the effects of three grazing regimes (sheep grazing, donkey grazing and sheep followed by donkey grazing) were investigated.

The main study site was the nature protection area “Ehemaliger August-Euler-Flugplatz von Darmstadt” located in the northern Upper Rhine Valley of Germany. This area served as a model for primarily calcareous inland sand ecosystems representing vegetation complexes of the Koelerion glaucae and the Armerion elongatae. Since 1999 the area has been grazed by sheep. Beginning in 2002 parts of the area are donkey-grazed and in 2003, at distinct areas, successive sheep and donkey grazing was established. For an analysis of the successional pathways, sand ecosystems with spontaneous succession in the vicinity of Darmstadt were investigated.

For the creation of a successional model of sand ecosystems, two tall grass species were chosen as representatives of mid-successional stages. *Stipa capillata* served as a representative of non-ruderalised mid-successional stages with high conservation value and high diversity of site-specific plant species. In contrast, *Calamagrostis epigejos* was chosen as a representative of low-diversity sites with ruderal grass-encroachment. Vegetation relevés of 23 permanent plots studied for 5-7 years were analysed in combination with the vegetation relevés of 71 plots where in addition soil analyses were carried out. Mineral and total nitrogen content as well as phosphate and potassium contents and pH values of the soil were determined. Additionally, moisture values calculated on the basis of Ellenberg indicator values of the plant species were analysed for each plot. It was shown that two successional pathways leading from Koelerion glaucae plots to mid-successional stages exist. In the case of dry conditions (optimal moisture value 3.2) and with low phosphate contents (< 15 mg * kg^{-1}) the non-ruderalisation pathway leading to Allio-Stipetum stands is most likely to occur. The

cover of *Calamagrostis epigejos* instead increases with increasing soil phosphate contents. This competitive grass species is not able to establish dominance stands if one of the following limits is reached: moisture value < 3.0, upper soil (0-10 cm soil depth): N_{total} < 0.04 %, K < 20 mg * kg^{-1}, lower soil (10-30 cm): N_{total} < 0.01 %, N_{min} < 0.5 mg * kg^{-1}, K < 10 mg * kg^{-1}. The conclusion can be drawn that site-specific plant communities are restricted to dry and nutrient-poor soils, and grass-encroachment is likely to occur in the case of nutrient-enriched plots.

As an experimental approach, the effect of nutrient addition on early successional stages of sand ecosystems was studied. A 5-times replicated randomised block design was carried out to examine the effects of organic carbon (C), phosphorus (P), nitrogen (low [n] and high dosages [N]), NP, NPK and NPK+ micro and macronutrients (NPKM) in relation to a control on 10 m² plots. Data on species composition, vegetation layer, above- and below-ground phytomass, vegetation height, seed production and soil nutrient content were analysed. The results show a two-fold increase of phanerogam phytomass production after N, NP, NPK and NPKM addition, indicating the existence of nutrient limitation. Species composition and phytodiversity were not significantly affected but a significant increase of the height of 6 species, a tendency for increase of 11 species, a decrease of 1 species and a significant increase of seed production for 3 species was shown. Therefore, nearly all species benefit from a nutrient intake and after 4 treatment years, competition is not yet strong enough for species to outcompete one another. With regard to a grazing impact, it can be concluded that accumulation of faeces or urine can lead to an increase of phytomass and ruderalisation, whereas a homogeneous distribution of dung pellets does not influence the vegetation.

For analysing the relationship between productivity, plant species richness and livestock diet in case of a sheep-grazed sand ecosystem two different approaches at two scales were used. At fine-grain scale (2 m²), productivity was measured by means of weighed aboveground phytomass, and data on livestock diet (grazed phytomass, crude protein content) were obtained. As a second means of analysing productivity, colour-infrared (CIR) aerial orthophotos were chosen and examined at fine-grain and at broad scale (79 m²). For measuring phytodiversity, at both scales, total numbers of vascular plant species and numbers of endangered vascular plant species were extracted from current vegetation relevés. A vegetational gradient from pioneer Koelerion glaucae stages and Koelerion glaucae grassland stages to consolidated Armerio-Festucetum trachyphyllae stands was investigated.

Mixed linear model analyses reveal an influence of the year on all variables and as shown by correlation and regression analyses, relationships between variables are not significant in every year. At fine-grain scale, species richness and number of endangered species are negatively related to productivity while crude protein content and grazed phytomass are positively related to productivity. At broad scale the diversity-productivity relationship is unimodal, with highest species numbers in Koelerion glaucae grassland stages. The numbers of endangered species are higher in all pioneer stages than in the consolidated Armerio-Festucetum trachyphyllae stages. It can be concluded that scale and year have a strong impact on the diversity-productivity relationship. A well-balanced management method has to be developed to combine the aims of nature conservation value (high diversity) and livestock nutrition.

In 2003 and 2004, the phytomass extraction and the diet preferences in the cases of sheep grazing, donkey grazing and sheep followed by donkey grazing were investigated with two closely related vegetation types (Armerio-Festucetum trachyphyllae and *Festuca trachyphylla/ duvalii*-community). In both vegetation types, each grazing approach was threefold replicated and paddocks of around 700 m² were grazed once a year for a short period. By means of 5 (respectively 4) 2-m² mini-exclosures per paddock, phytomass was sampled on the ungrazed plots and adjacent grazed plots and each sample was differentiated into the three plant functional types graminoids, Fabaceae and other herbs. It turned out that total phytomass extraction is highest with the two-species approach, while the quantitative phytomass extraction by sheep and donkeys is not significantly different. Concerning preferences for particular plant functional types, sheep extract more percentual phytomass of herbs than of graminoids, whereas donkeys select for Fabaceae. For successive two-species grazing no difference between the grazing extraction of all plant functional types is observed. As a consequence, successive two-species grazing is an ideal method for both reducing grass-encroachment and achieving maximum phytomass extraction, and thus to restore and to preserve high phytodiversity.

Within the same threefold-replicated sampling design at the 700 m² paddocks, the effects of the three grazing regimes (sheep grazing [s], donkey grazing [d], successive two-species grazing [s+d]) on the vegetation were investigated. During 2002 and 2005 the vegetation was recorded by 1629 relevés of 25 m² plots. Additionally, data on species composition, nitrogen

input and phytomass were obtained at donkey-generated microsites (faeces- and urine accumulation sites, wallows, scratch sites).

Mixed linear model analyses revealed a strong influence of “year” and “vegetation type” on vegetation parameters. Species number, especially therophytes, and gap creation were significantly higher for donkey grazing than for sheep grazing. The vegetation layers were influenced by all treatments but cover of bryophytes and graminoids was influenced to a stronger extent for donkey grazing than for sheep grazing. Successive two-species grazing was not significantly different from the other treatments. Concerning donkeys’ faeces accumulation sites, a nitrogen input of 223 kg N * ha^{-1} at 4 % of the paddock could be observed. Although the phytomass at faeces sites was lower after 15 weeks and identical after 45 weeks in relation to controls, the species composition suggests a ruderalisation tendency. In conclusion, sheep grazing is adequate as a conservation method for rather intact sand ecosystems while donkey grazing is ideal for an intensive gap creation in case of consolidated stages. Due to a partial ruderalisation of the paddock, donkey grazing should not be repeated. Successive two-species grazing is also an adequate management method, but is probably of greater importance in ruderalised areas.

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This thesis first explained the occurrence of a ruderalisation and a non-ruderalisation pathway in inland sand ecosystems. While for early successional stages mainly nitrogen was proved to be the limiting factor for phytomass production, species composition was not significantly affected by an enhanced nutrient supply. In mid-successional stages low phosphate availability and dry conditions are decisive for the non-ruderalisation pathway to be taken. Productivity was found to be unimodally related to phytodiversity, with highest phytodiversity at Koelerion glaucae grassland stages. To preserve the open structure of these rather intact habitats, sheep grazing turned out to be an ideal management method. Donkey grazing is a very effective method for gap creation at more consolidated stages but due to the occurrence of ungrazed faeces accumulation sites, parts of the paddock can become ruderalised after repeated donkey grazing.

The ruderalisation pathway of succession will develop in case of an enhanced nutrient availability. Successive two-species grazing is inferred to be the best management method for restoring these areas and directing the ruderal successional pathway into the non-ruderal direction.

Zusammenfassung

Sandökosysteme des Binnenlandes zählen zu den am stärksten gefährdeten Habitaten Zentraleuropas. Besonders in jüngster Vergangenheit konnten Abnahmen standorttypischer Pflanzenarten und Ruderalisierungtendenzen verzeichnet werden. Dies wird häufig mit einem verstärkten Nährstoffeintrag, aber auch mit der Aufgabe extensiver Landnutzung und damit einhergehender spontaner Sukzession, in Verbindung gebracht.

Die Entwicklung eines Sukzessionsmodells für Binnenland-Sandökosysteme war für diese Arbeit von zentraler Bedeutung und diente als Grundlage für die Untersuchung von Nährstoffeinflüssen und Produktivitäts-Diversitätsbeziehungen. Da Sandökosysteme maßgeblich von einem Beweidungseinfluss abhängig sind, wurden die Auswirkungen dreier Beweidungsformen (Schafbeweidung, Eselbeweidung, sukzessive Schaf-Eselbeweidung) auf die Vegetation untersucht.

Hauptuntersuchungsgebiet war das in der nördlichen Oberrheinebene gelegene Naturschutzgebiet „Ehemaliger August-Euler-Flugplatz von Darmstadt". Das Gebiet kann als Modell für primär kalkreiche Sandökosysteme des Binnenlandes angesehen werden und beinhaltet Vegetationskomplexe des Koelerion glaucae und des Armerion elongatae. Seit 1999 wird das Gebiet mit Schafen beweidet, auf einzelnen Teilbereichen findet seit 2002 eine Eselbeweidung statt. Im Jahr 2003 wurde auf Teilflächen eine sukzessive Schaf-Eselbeweidung etabliert. Die Entwicklung des Sukzessionsmodells beruht auf Untersuchungen unbeweideter Sandökosysteme mit spontaner Sukzession in der Umgebung von Darmstadt.

Zur Entwicklung des Sukzessionsmodells wurden zwei hochwüchsige Grasarten herangezogen, die als typische Vertreter mittlerer Sukzessionsstadien in Sandökosystemen gelten können. Das Auftreten von *Stipa capillata* repräsentiert dabei nicht-ruderalisierte Flächen von hoher naturschutzfachlicher Bedeutung wohingegen *Calamagrostis epigejos* als Repräsentant artenarmer, von ruderalen Gräsern dominierter, Bestände angesehen werden kann. Eine Auswertung der Vegetationsaufnahmen von 23 bereits seit 5-7 Jahren untersuchten Dauerflächen fand gemeinsam mit den Aufnahmen von 71 weiteren Flächen statt, auf denen zusätzlich Bodenuntersuchungen stattfanden. Die Bodenuntersuchungen beinhalteten eine Bestimmung des pH-Wertes, des mineralischen Stickstoffgehaltes und des Gesamtstickstoffgehaltes, sowie des Phosphat- und Kaliumgehaltes. Mit Hilfe der Ellenberg'schen Feuchtezahlen wurde für jede Fläche ein mittlerer Feuchtewert berechnet.

Als Ergebnis zeigt sich, dass zwei verschiedene Sukzessionspfade zwischen Koelerion glaucae-Gesellschaften und mittleren Sukzessionsstadien unterschieden werden können. Bei trockenen Bedingungen (optimaler Feuchtewert 3.2) und niedrigen Phosphatgehalten (< 15 mg * kg^{-1}) ist eine Entwicklung des nicht-ruderalisierten Pfades zu prognostizieren, der zur Ausbildung von Allio-Stipetum-Beständen führt. Die Deckung von *Calamagrostis epigejos* ist hingegen positiv mit dem Phosphatgehalt korreliert. Bei Unterschreitung der folgenden Grenzwerte ist *C. epigejos* nicht in der Lage, Dominanzbestände zu entwickeln: Feuchtezahl < 3.0, Oberboden (0-10 cm Bodentiefe): N_{total} < 0.04 %, K < 20 mg * kg^{-1}, Unterboden (10-30 cm): N_{total} < 0.01 %, N_{min} < 0.5 mg * kg^{-1}, K < 10 mg * kg^{-1}. Dementsprechend lässt sich rückschließen, dass die standorttypischen Pflanzengesellschaften auf trockene und nährstoffarme Böden beschränkt sind, wohingegen auf nährstoffreicheren Flächen ruderale Grasarten zur Dominanz gelangen können.

Die Auswirkungen von Nährstoffeinträgen auf die Vegetation früher Sukzessionsstadien wurden im Rahmen eines experimentellen Ansatzes mit Hilfe eines fünffach replizierten randomisierten Blockdesigns untersucht. Auf jeweils 10 m² großen Flächen fand eine Applikation von organischem Kohlenstoff (C), Phosphor (P), Stickstoff in geringer (n) und in hoher (N) Dosis, NP, NP+ Kalium (NPK) und NPK + Mikro- und Makronährstoffe (NPKM) statt. Die Auswirkungen der Nährstoffgaben auf die Artenzusammensetzung, Deckung der Vegetationsschichten, ober- und unterirdische Phytomasse, Wuchshöhe und Samenproduktion einzelner Arten sowie auf die Nährstoffgehalte des Bodens wurden analysiert. Eine Verdopplung der Phanerogamen-Phytomasse bei Zugabe von N, NP, NPK oder NPKM und damit eine Nährstofflimitierung der Böden konnte nachgewiesen werden. Während die Artenzusammensetzung und die Phytodiversität keine Effekte aufweisen, zeigt sich für 6 Arten eine signifikante Erhöhung der Wuchshöhe, bei weiteren 11 Arten eine tendenzielle Erhöhung der Wuchshöhe und für eine Art eine signifikant geringere Wuchshöhe bei NPKM-Zugabe. Bei drei Arten ist die Samenproduktion im Fall intensiver Nährstoffzufuhr signifikant erhöht. Daher lässt sich rückschließen, dass nach vier Behandlungsjahren nahezu alle Pflanzenarten von Nährstoffeinträgen profitieren, die Konkurrenz jedoch noch nicht stark genug ausgeprägt ist, um zur Verdrängung einzelner Arten zu führen. Überträgt man die Ergebnisse auf die Auswirkungen eines Nährstoffeintrages durch Beweidung, lässt sich rückschließen, dass es an Stellen mit akkumuliertem Faeces- oder Urineintrag zu einer Erhöhung der Phytomasse und letztlich zu Ruderalisierung kommen kann, wohingegen bei

einer homogenen Verteilung von Exkrementen keine deutlichen Auswirkungen auf die Vegetation zu erwarten sind.

Während eines dreijährigen Untersuchungszeitraums konnten die Beziehungen zwischen Produktivität, Phytodiversität und Tierernährung im Falle von schafbeweideten Sandökosystemen auf zwei verschiedenen Skalenebenen analysiert werden. Auf der Mikroskala (2 m²) wurde die oberirdische Phytomasse als Maß der Produktivität herangezogen, und zur Untersuchung der Tierernährung der prozentuale Fraßanteil und der Rohproteingehalt der Phytomasse ermittelt. Die Produktivität konnte zusätzlich auch mit Hilfe von Farb-Infrarot (CIR)-Luftbildern bestimmt werden, dies geschah sowohl auf der Mikroskala als auch auf der Makroskala (79 m²). Auf beiden Skalenebenen dienten Vegetationsaufnahmen als Grundlage zur Ermittlung der Phytodiversität und der Anzahl an Rote Liste-Arten, wobei ein Vegetationsgradient von frühen Koelerion glaucae-Pionierstadien über grasreichere Koelerion glaucae-Stadien bis hin zu konsolidierten Armerio-Festucetum trachyphyllae-Beständen abgedeckt war. Die gemischt-linearen Modelle zeigen eine starke Beeinflussung der Variablen durch das jeweilige Untersuchungsjahr, und auch die Ergebnisse der Korrelationen und Regressionen zwischen den Variablen sind jahresabhängig. Während auf der Mikroskala die Artenzahl und die Anzahl der gefährdeten Arten negativ mit der Produktivität korreliert sind, weist der Fraßanteil einen positiven Zusammenhang zur Produktivität auf. Auf der Makroskala zeigt sich hingegen ein unimodaler Zusammenhang zwischen Produktivität und Diversität mit einem Pflanzenartenmaximum in grasreicheren Koelerion glaucae-Beständen. Die Anzahl der gefährdeten Pflanzenarten ist in allen Koelerion glaucae-Gesellschaften höher als im Armerio-Festucetum trachyphyllae. Demnach wirken sich sowohl die Skalenebenen als auch das Untersuchungsjahr stark auf den Zusammenhang zwischen Produktivität und Diversität aus. Außerdem erscheint die Etablierung eines ausgewogenen Weideregimes notwendig, das sowohl Naturschutzaspekte als auch eine adäquate Tierernährung gewährleisten kann.

Die Untersuchung des prozentualen Phytomasseentzugs und der Fraßpräferenzen im Fall von drei unterschiedlichen Beweidungsformen (Schafbeweidung, Eselbeweidung, sukzessive Schaf-Eselbeweidung) fand in den Jahren 2003 und 2004 in zwei eng verknüpften Vegetationstypen (Armerio-Festucetum trachyphyllae und *Festuca trachyphylla/duvalii*-Gesellschaft) statt. In beiden Vegetationstypen war jeder Beweidungsansatz dreifach repliziert, und die ca. 700 m² großen Koppeln wurden einmal jährlich beweidet. Mit Hilfe von

2 m² großen Mini-Exclosures konnten auf jeder Koppel 5 (bzw. 4) unbeweidete Teilflächen erzeugt werden. Nach der Beweidung wurden die Phytomasse der unbeweideten Fläche und der Weiderest einer unmittelbar angrenzenden beweideten Fläche abgeerntet und in die Gruppen Grasartige, Leguminosen und sonstige Kräuter getrennt. Es zeigte sich, dass trotz gleich starken Verbisses der Gesamtphytomasse durch Schafe und Esel ein signifikant stärkerer Phytomasseentzug im Fall der sukzessiven Schaf-Eselbeweidung erzielt werden kann. Schafe verbeißen jedoch Kräuter mit stärkerer Intensität als Gräser, wohingegen Esel Leguminosen bevorzugen. Im Fall der sukzessiven Schaf-Eselbeweidung werden alle drei funktionellen Pflanzengruppen mit gleicher Intensität verbissen. Daher erscheint insbesondere die sukzessive Schaf-Eselbeweidung als geeignete Pflegemaßnahme zur Erzeugung und zum Erhalt artenreicher Ökosysteme, da ruderale Grasarten durch eine starke Reduktion der Phytomasse dezimiert werden können.

Die Auswirkungen dieser drei Beweidungsformen (Schafbeweidung, Eselbeweidung, sukzessive Schaf-Eselbeweidung) auf die Vegetation der ca. 700 m² großen Koppeln wurden zwischen 2002 und 2005 im Rahmen desselben dreifach-replizierten experimentellen Ansatzes untersucht. Durch 1629 Vegetationsaufnahmen jeweils 25 m² großer Einzelflächen wurden Veränderungen der Vegetation erfasst und zusätzlich auf speziellen Sonderstandorten der Eselbeweidung (Faeces- und Urin-Akkumulationsstellen, Wälzkuhlen, Scharrstellen) Daten zur Zusammensetzung der Vegetation, sowie zur Phytomasse und zum Stickstoffeintrag erhoben. Die Auswertung von gemischt-linearen Modellen weist einen starken Einfluss des Jahres und des Vegetationstyps auf. Bei Eselbeweidung zeigt sich im Vergleich zu Schafbeweidung eine Erhöhung der Artenzahl, insbesondere der Zahl einjährigen Arten, sowie eine verstärkte Entstehung von Offenbodenstellen. Alle Beweidungsformen zeigen deutliche Einflüsse auf die Deckung der unterschiedlichen Vegetationsschichten; Moos- und Grasschicht werden jedoch durch Eselbeweidung deutlicher dezimiert als durch Schafbeweidung. Die Ergebnisse der sukzessiven Schaf-Eselbeweidung unterscheiden sich nicht signifikant von denen der beiden anderen Beweidungsformen. Im Falle der bei Eselbeweidung auftretenden Faeces-Akkumulationsstellen kommt es auf 4 % der Fläche zu einem Stickstoffeintrag von 223 kg N * ha^{-1}. 15 Wochen nach Beweidung ist die Phytomasse auf den Faecesstellen signifikant erniedrigt, nach 45 Wochen kann kein Unterschied in der Phytomasse mehr festgestellt werden. Die Artenzusammensetzung weist allerdings auf eine Ruderalisierungstendenz der Vegetation der Faeces-Akkumulationsstellen hin. Daher kann das Fazit gezogen werden, dass Schafbeweidung vor allem als erhaltende

Maßnahme zur Pflege von vergleichsweise intakten Sandökosystemen geeignet ist, wohingegen Eselbeweidung besonders zur Schaffung offener Stellen auf konsolidierteren Flächen herangezogen werden kann. Da aber bei Eselbeweidung eine teilweise Ruderalisierung der Flächen möglich ist, ist diese Maßnahme nicht zur häufigen Wiederholung geeignet. Sukzessive Schaf-Eselbeweidung kann zur Pflege von Sandökosystemen eingesetzt werden, gewinnt aber erst mit stärkerer Ruderalisierung der Gebiete zunehmend an Bedeutung.

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Im Rahmen dieser Arbeit konnte erstmalig ein Modell für das Auftreten von ruderalisierten und nicht-ruderalisierten Sukzessionspfaden in Sandökosystemen entwickelt werden. Obwohl die Phytomasseproduktion früher Sukzessionsstadien durch Stickstoff limitiert ist, zeigt sich nach 4 Behandlungsjahren noch keine signifikante Änderung der Artenzusammensetzung durch Nährstoffeinträge. In mittleren Sukzessionsstadien beeinflusst hingegen neben der Trockenheit auch der Nährstoffgehalt des Bodens den Verlauf der Sukzession. Nur bei niedrigen Phosphatgehalten und trockenen Standorten ist die Entwicklung des nicht-ruderalisierten Sukzessionspfades zu prognostizieren. Die Produktivität steht dabei in unimodaler Beziehung zur Pflanzendiversität mit maximalem Pflanzenartenreichtum in grasreicheren Koelerion glaucae Stadien. Zur Offenhaltung dieser vergleichsweise intakten Sandökosysteme erweist sich Schafbeweidung als eine ideale Maßnahme. Eselbeweidung hingegen ist zwar sehr effektiv zur Schaffung lückiger Bodenstrukturen, durch das Anlegen von unbeweideten Faeces-Akkumulationsstellen können bei wiederholter Eselbeweidung jedoch Teile der Fläche ruderalisieren. Bei erhöhten Nährstoffgehalten des Bodens wird mit hoher Wahrscheinlichkeit der ruderalisierte Sukzessionspfad eingeschlagen der zur Entstehung artenarmer Bestände mit Dominanz hochwüchsiger Grasarten führt. Zur Umlenkung des ruderalisierten Sukzessionspfades in Richtung nicht-ruderalisierter Bestände, erscheint die sukzessive Schaf-Eselbeweidung als die am besten geeignete Maßnahme.

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Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Ich habe noch keinen Promotionsversuch unternommen.

Darmstadt, 20.12.2005